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A COLLECTION OF HYDROIDS
FROM MOÇAMBIQUE, EAST AFRICA

By
N. A. H. MILLARD
&
J. BOUILLON

Cape Town Kaapstad

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Université Libre de Bruxelles

(With 9 figures)

[MS accepted 30 May 1973]

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INTRODUCTION

This paper is the second part of an account of the collection made by the second author and his colleagues during expeditions to the Seychelles in 1960 and to the east coast of Africa in 1969. The hydroids of the Seychelles, which comprised the first part, are described by Millard & Bouillon (1973).

Most of the collection comes from the southern part of Moçambique: from Inhaca Island and Ilha dos Portugueses, which lie to the east of Lourenço Marques in Delagoa Bay, but there is also material from Santa Carolina, a small island further north between the larger Ilha do Bazaruto and the mainland. The area thus lies on the border of the tropics and is in general under the influence of the warm southward-flowing Moçambique current, although the temperature of the coastal waters is somewhat less due to the presence of an inshore northward-flowing counter-current. Macnae & Kalk (1958) give a temperature of approximately 26°C for the Moçambique current and 20°C for the eastern shores of Inhaca Island, whereas the water in Delagoa Bay itself tends to be warmer due to the heating of the sun during the day.

The position of the collecting stations is listed as follows:

Inhaca, Station. On the west coast of Inhaca Island. 26°03'S/32°54'E.

Inhaca, Barreira Vermelha. On the west coast of Inhaca Island.
26°02'S/32°54'E.

Ilha dos Portugueses. An island to the north-west of Inhaca Island, in Delagoa Bay. 25°58'S/32°55'E.

Inhaca Est.

Inhaca, Saco. A bay on the south coast of Inhaca Island. 26°03'S/32°56'E.

Cabo da Inhaca. The most north-easterly point of the island. 25°58'S/32°59'E.

Inhaca Est (dragage, 10–15 m).

Inhaca, Ponta Torres. The most south-easterly point of the island. 26°05'S/32°57'E.

Santa Carolina. An island further north on the coast of Moçambique. 21°37'S/35°20'E.

An account of the marine ecology of Inhaca Island will be found in Macnae & Kalk (1958), while some of the hydroids from the area were described by Millard (1958, 1959).

Since many of the species from southern Africa have already been described or are too well known to warrant description, only certain ones are described in detail and illustrated. All are recorded in the list which follows. As in the previous paper, unidentifiable material is not recorded.

The expedition was financed by the Université Libre de Bruxelles, the Musée Royal de l'Afrique Centrale (Tervuren), the Centre Belge d'Océanographie and the Belgian Ministry of Education and Culture.

The collection is the property of the Musée Royal de l'Afrique Centrale, where the type of the single new species has been deposited.

LIST OF MATERIAL AND LOCALITIES

*Species marked with an asterisk are described or discussed in the systematic section.

†Species marked with a dagger are new records for Africa south of 20°S. Lat.

Family **Myriotheilidae**

Myriotheila sp.

Santa Carolina: a single infertile specimen 0,8 mm in total height.

Family **Tubulariidae**

**Ectopleura bethae* (Warren, 1908)

Inhaca: a rich, fertile colony.

Zyzyzus solitarius (Warren, 1906)

Cabo da Inhaca: several hydranths, one fertile, growing in a sponge.

Santa Carolina: one fertile hydranth in sponge.

Family **Cladocorynidae**

**Cladocoryne floccosa* Rotch, 1871

Ilha dos Portugueses: a rich fertile colony on *Dynamena crisioides*.

Inhaca, Saco: an infertile colony on *Lytocarpus philippinus*.

Inhaca, Ponta Torres: a rich colony with a few fertile hydranths.

Family Halocordylidae

Halocordyle disticha (Goldfuss, 1820)

Inhaca, Ponta Torres: stems reaching 56 mm, some with young gonophores.

Santa Carolina: fertile stems reaching 35 mm.

Family Corynidae

**Coryne ?pusilla* Gärtner, 1774.

Inhaca Est: an infertile colony on weed.

Inhaca, Ponta Torres: infertile colonies.

**Sphaerocoryne bedoti* Pictet, 1893

Santa Carolina: a single infertile hydranth detached from substratum.

Family Cladonemidae

†? *Cladonema* sp.

Inhaca: three young, infertile hydranths reaching 0,8 mm.

Family Solanderiidae

† *Solanderia minima* (Hickson, 1903)

Santa Carolina: an infertile colony 70 mm in height and 70 mm in spread.

Family Zancleidae

†* *Zanclea* sp.

Inhaca, coral reef west of Station: an infertile colony commensal on a coral (colony 1).

Inhaca, coral reef west of Station: a fertile colony from coral reef, growing with a polyzoan (colony 2).

Inhaca, Barreira Vermelha: two colonies, one fertile, on polyzoan (colonies 3 and 4).

Family Clavidae

Corydendrium parasiticum (Linnaeus, 1767)

Inhaca, Station: an infertile colony reaching 46 mm.

Inhaca Est: a young colony reaching 8 mm.

Inhaca, Saco: a rich, but infertile, colony reaching 56 mm.

Inhaca, Ponta Torres: rich, but infertile, colonies reaching 59 mm.

†* *Rhizogeton nudum* Broch, 1909

Inhaca, Station: a fertile colony on weed.

Ihla dos Portugueses: a few infertile hydranths.

Santa Carolina: a few infertile hydranths.

†* *Turritopsis nutricula* (McCrady, 1856)

Inhaca, Station: a young, infertile colony.

Inhaca Est (dragage): a few young hydranths.

Santa Carolina: several small colonies, one with young medusae.

Family Cytaeidae

Cytaeis nassa (Millard, 1959)

Ihla dos Portugueses: fertile colonies on shells of *Nassa fenestrata*.

Family **Eudendriidae**

**Eudendrium capillare* Alder, 1856

Inhaca, Barreira Vermelha: one infertile colony.

Cabo da Inhaca: one infertile colony.

Inhaca, Ponta Torres: three fertile colonies.

Santa Carolina: one infertile colony.

†**Eudendrium motzkossowskiae* Picard, 1951

Inhaca, Saco: one infertile colony.

Inhaca, Ponta Torres: three colonies, two male and one infertile.

Santa Carolina: one infertile colony.

**Eudendrium ramosum* (Linnaeus, 1758)

Inhaca Est: four colonies, three of them fertile.

Inhaca, Saco: one infertile colony.

Cabo da Inhaca: one infertile colony.

Inhaca, Ponta Torres: eight colonies, five of them fertile.

Family **Hydractiniidae**

**Hydractinia diogenes* Millard, 1959

Inhaca, Station: a fertile colony on hermit shell.

Inhaca, Ponta Torres: a fertile colony on empty shell.

**Podocoryne ?carnea* M. Sars, 1846

Inhaca Est (dragage): a female colony on weed.

*Incertae sedis (1)

Inhaca Est (dragage): a few minute hydranths on polyzoan.

*Incertae sedis (2)

Inhaca, Barreira Vermelha: an infertile colony.

†*Incertae sedis (3) *Lineolaria* sp.

Inhaca, Barreira Vermelha: an infertile colony.

Family **Aequoreidae**

Aequorea africana Millard, 1966

Ilha dos Portugueses: an infertile colony with a few contracted hydranths.

Family **Calicellidae**

†*Egmundella amirantensis* Millard & Bouillon, 1973

Inhaca, Station: two infertile colonies.

Ilha dos Portugueses: infertile colonies on *Dynamena crisioides*.

Santa Carolina: an infertile colony on *Dynamena crisioides*.

Family **Haleciidae**

Halecium halecinum (Linnaeus, 1758)

Inhaca Est (dragage): a small female colony reaching 4 mm, on weed.

Halecium inhacae Millard, 1958

Inhaca, Station: a fertile colony reaching 4 mm.

Inhaca Est: fertile colonies on weed, reaching 3 mm.

Inhaca, Ponta Torres: rich fertile colonies on weed, reaching 3,5 mm.

Halecium lankesteri (Browne, 1890)

Santa Carolina: a small male colony reaching 2,6 mm, on worm tubes and other hydroids, and a rich female colony reaching 1,5 mm, on weed.

**Halecium tenellum* Hincks, 1861

Ilha dos Portugueses: an infertile colony reaching 3 mm.

Cabo da Inhaca: fertile colonies reaching 5 mm.

Inhaca Est (dragage): an infertile colony reaching 5 mm.

Inhaca, Ponta Torres: a rich fertile colony reaching 3 mm.

†*Hydrodendron gardineri* (Jarvis, 1922)

Cabo da Inhaca: several infertile colonies on the ascidian *Pyura* and on the mussel *Perna perna*.

**Hydrodendron sympodiiformis* n. sp.

Inhaca, Ponta Torres: a very rich fertile colony on weed.

Family **Campanulariidae***Campanularia crenata* (Hartlaub, 1901)

Inhaca, Station: an infertile colony on weed.

Inhaca, Barreira Vermelha: a fertile colony on weed.

Inhaca, Ponta Torres: a rich fertile colony on weed.

**Campanularia delicata* (Trebilcock, 1928)

Cabo da Inhaca: fertile colonies on weed.

Inhaca Est (dragage): an infertile colony on weed.

Campanularia integra MacGillivray, 1842

Inhaca Est: rich fertile colonies on weed.

Inhaca Est (dragage): a rich fertile colony on weed.

Inhaca, Ponta Torres: rich fertile colonies on weed.

Campanularia laminacarpa Millard, 1966

Cabo da Inhaca: an infertile colony epizootic on *Thyroscyphus aequalis*.

Campanularia morgansi Millard, 1957

Cabo da Inhaca: fertile colonies on *Pyura* and *Perna perna*.

Clytia gravieri (Billard, 1904)

Inhaca, Station: two colonies, one fertile, with branched and stolonial stems.

Inhaca, Barreira Vermelha: a fertile colony with stolonial and slightly branched stems, on weed.

Ilha dos Portugueses: an infertile stolonial colony.

Cabo da Inhaca: slightly branched stems with one gonotheca.

Inhaca, Ponta Torres: slightly branched infertile stems reaching 14 mm.

Santa Carolina: several stolonial colonies on weed, some fertile.

Clytia hemisphaerica (Linnaeus, 1767)

Inhaca, Station: several colonies, some fertile, with gonothecae of the *johnstoni* type.

Inhaca, Barreira Vermelha: fertile colonies on weed with gonothecae of the *johnstoni* type.

Ihla dos Portugueses: fertile colonies on weed with gonothecae of the *johnstoni* type.

Cabo da Inhaca: two infertile colonies.

Inhaca Est (dragage): infertile colonies on weed.

Inhaca, Ponta Torres: several infertile colonies.

Santa Carolina: several colonies on weed, one fertile, with gonothecae of the *johnstoni* type.

†*Clytia latithea* Millard & Bouillon, 1973

Cabo da Inhaca: a small infertile colony reaching 6 mm.

Clytia paulensis (Vanhöffen, 1910)

Inhaca, Saco: an infertile colony epizootic on *Lytocarpus philippinus*.

**Clytia* sp.

Inhaca Est (dragage): a small infertile colony on weed.

Obelia bicuspidata Clarke, 1875

Inhaca, Station: infertile stems reaching 4 mm, on weed.

Ihla dos Portugueses: infertile stems reaching 5 mm.

Obelia dichotoma (Linnaeus, 1758)

Ihla dos Portugueses: rich fertile colonies reaching 9 mm, on weed and epizootic on *Dynamena crisioides*.

Cabo da Inhaca: infertile colonies reaching 8 mm.

Inhaca, Ponta Torres: rich fertile colonies reaching 7 mm, on weed.

Santa Carolina: an infertile colony reaching 7 mm.

Obelia geniculata (Linnaeus, 1758)

Inhaca, Station: a rich infertile colony on weed.

Inhaca Est: rich fertile colonies reaching 6 mm, on weed.

Cabo da Inhaca: a fertile colony on a gastropod shell.

Inhaca, Ponta Torres: fertile colonies reaching 5 mm, on weed.

Family Lafoeidae

Hebella furax Millard, 1957

Inhaca, Barreira Vermelha: an infertile colony epizootic on *Halopteris polymorpha*.

Ihla dos Portugueses: an infertile colony epizootic on *Halopteris polymorpha*.

Hebella scandens (Bale, 1888)

Ihla dos Portugueses: infertile colonies epizootic on *Dynamena crisioides* and *D. cornicina*.

Cabo da Inhaca: an infertile colony epizootic on *Dynamena quadridentata*.

Inhaca Est (dragage): a rich colony epizootic on *Sertularia linealis*, with a few gonothecae.

Inhaca, Ponta Torres: an infertile colony epizootic on *Dynamena crisioides*.

Santa Carolina: infertile colonies epizootic on *Dynamena crisioides*.

**Scandia mutabilis* (Ritchie, 1907)

Inhaca Est: an infertile colony epizootic on *Eudendrium ramosum*.

Cabo da Inhaca: infertile colonies epizootic on various hydroids.

Inhaca, Ponta Torres: infertile colonies epizootic on *Halocordyle disticha*, *Eudendrium ramosum* and *Idiellana pristis*.

Family **Syntheciidae**

Hincksella corrugata Millard, 1958

Inhaca Est (dragage): one infertile stem of 3 mm.

Santa Carolina: an infertile colony reaching 10 mm.

Synthecium ?elegans Allman, 1872

Santa Carolina: five infertile stems reaching 15 mm.

Family **Sertulariidae**

**Abietinaria laevimarginata* (Ritchie, 1907)

Ihla dos Portugueses: fertile colony on weed.

Inhaca Est (dragage): infertile colonies on weed.

Amphisbetia minima (D'Arcy Thompson, 1879)

Inhaca Est: rich fertile colonies reaching 3 mm, on weed.

Inhaca Est (dragage): an infertile colony reaching 2,5 mm, on weed.

Inhaca, Ponta Torres: rich fertile colonies reaching 3 mm, on weed.

†**Diphasia digitalis* (Busk, 1852)

Inhaca Est: a branched stem of 7 mm and three smaller unbranched ones, all infertile.

Inhaca, Ponta Torres: infertile branched and unbranched stems reaching 44 mm.

**Diphasia tetraglochina* Billard, 1907

Inhaca Est: an infertile colony reaching 2,5 mm, on weed.

Cabo da Inhaca: an infertile colony reaching 7 mm.

Inhaca Est (dragage): an infertile colony reaching 3 mm, on weed.

Dynamena cornicina McCrady, 1858

Ihla dos Portugueses: unbranched fertile stems reaching 4 mm.

Inhaca Est: two unbranched infertile stems reaching 9 mm.

Santa Carolina: several branched infertile stems reaching 60 mm, and two rich fertile colonies with unbranched stems reaching 9 mm.

**Dynamena crisioides* Lamouroux, 1824

Ihla dos Portugueses: many tall infertile stems of var. *gigantea* reaching 159 mm.

Inhaca, Saco: two infertile stems of normal variety reaching 13 mm.

Inhaca, Ponta Torres: infertile stems of normal variety reaching 20 mm.

Santa Carolina: many stems, reaching 160 mm, some fertile, including normal variety, var. *gigantea* and var. *alternata*.

Dynamena obliqua Lamouroux, 1816

Inhaca Est (dragage): an infertile colony reaching 11 mm, on weed.

Inhaca, Ponta Torres: infertile stems reaching 4 mm, on weed.

Dynamena quadridentata (Ellis & Solander, 1786)

Ihla dos Portugueses: a fertile female colony reaching 6 mm, on weed.

Inhaca, Saco: infertile stems reaching 5 mm.

Cabo da Inhaca: infertile stems reaching 7 mm, on *Pyura*, *Perna perna* and weed.

Inhaca Est (dragage): infertile stems reaching 5 mm, on weed.

Inhaca, Ponta Torres: infertile stems reaching 4 mm, on weed.

Santa Carolina: infertile stems reaching 3 mm, on weed.

Idiellana pristis (Lamouroux, 1816)

Inhaca, Station: several young colonies reaching 21 mm, on a bivalve.

Inhaca, Barreira Vermelha: two infertile stems reaching 19 mm.

Inhaca, Ponta Torres: infertile stems reaching 52 mm.

Santa Carolina: two infertile stems reaching 45 mm.

Sertularella mediterranea asymmetrica Millard, 1958

Inhaca Est: a fertile colony reaching 6 mm.

Inhaca, Ponta Torres: a fertile colony reaching 7 mm, on weed.

Sertularia distans (Lamouroux, 1816)

Inhaca, Station: unbranched stems reaching 12 mm, some fertile, on weed and a shell.

Inhaca, Ponta Torres: unbranched, infertile stems reaching 4 mm, on weed.

Santa Carolina: unbranched, infertile stems reaching 4 mm, on weed.

Sertularia ligulata Thornely, 1904

Inhaca, Station: infertile stems reaching 27 mm.

Inhaca Est (dragage): infertile stems reaching 8 mm, on weed.

Santa Carolina: infertile stems reaching 10 mm.

**Sertularia longa* (Millard, 1958)

Ihla dos Portugueses: fertile colonies reaching 3 mm, on weed.

Inhaca Est (dragage): infertile colonies on weed.

**Sertularia marginata* (Kirchenpauer, 1864)

Inhaca, Ponta Torres: infertile stems reaching 16 mm.

Sertularia turbinata (Lamouroux, 1816)

Inhaca, Station: an infertile colony reaching 6 mm.

Thyroscyphus aequalis Warren, 1908

Cabo da Inhaca: several infertile stems reaching 39 mm.

Thyroscyphus fruticosus (Esper, 1793)

Inhaca, Station: fertile fragments reaching 50 mm.

Family **Plumulariidae***Antennella secundaria* (Gmelin, 1791)

Inhaca Est: infertile stems reaching 5 mm.

Inhaca, Saco: infertile stems reaching 12 mm.

Inhaca, Ponta Torres: stems reaching 10 mm, some fertile.

Santa Carolina: stems reaching 8 mm, some fertile.

† *Dentitheca bidentata* (Jäderholm, 1920)

Inhaca, Barreira Vermelha: infertile stems reaching 11 mm.

Halopteris glutinosa (Lamouroux, 1816)

Inhaca Est: many stems, some fertile, reaching 17 mm.

Inhaca, Ponta Torres: stems reaching 18 mm, some fertile.

Halopteris polymorpha (Billard, 1913)

Inhaca Station: fertile stems reaching 11 mm.

Inhaca, Barreira Vermelha: an infertile stem of 9 mm.

Ihla dos Portugueses: stems reaching 16 mm, some fertile.

Inhaca, Ponta Torres: an infertile stem of 16 mm.

Santa Carolina: many infertile stems reaching 22 mm.

Kirchenpaueria irregularis (Millard, 1958)

Santa Carolina: two infertile colonies with fascicled branched stems reaching 13 mm.

† *Monostaechas quadridens* (McCrary, 1857)

Cabo da Inhaca: stems reaching 13 mm, some fertile, on *Pyura*, *Perna perna* and a sponge.

Inhaca, Ponta Torres: infertile stems reaching 8 mm.

Santa Carolina: many infertile stems reaching 13 mm.

Oswaldella nova (Jarvis, 1922)

Santa Carolina: infertile colonies epizootic on *Halopteris polymorpha*.

Plumularia filicaulis Kirchenpauer, 1876

Inhaca Est: fertile stems reaching 5 mm, on weed.

Inhaca Est (dragage): an infertile colony reaching 2,5 mm, on weed.

Inhaca, Ponta Torres: fertile colonies reaching 5 mm, on weed.

†* *Plumularia obliqua* (Johnston, 1847)

Inhaca Est: an infertile colony reaching 4 mm, on weed.

Inhaca Est (dragage): an infertile colony reaching 5 mm, on weed.

† *Plumularia pennycuikae* Millard & Bouillon, 1973

Santa Carolina: two infertile colonies reaching 13 mm.

Plumularia setacea (Linnaeus, 1758)

Cabo da Inhaca: abundant fertile stems reaching 22 mm, on *Perna perna*, sponges and other substrata.

Santa Carolina: fertile stems reaching 20 mm.

† *Plumularia strictocarpa* Pictet, 1893

Santa Carolina: several fertile colonies reaching 10 mm.

Plumularia warreni Stechow, 1919

Inhaca, Ponta Torres: a fertile colony reaching 5 mm, on weed.

Santa Carolina: fertile colonies reaching 15 mm.

Plumularia wasini Jarvis, 1922

Santa Carolina: an infertile colony reaching 13 mm.

Pycnotheca mirabilis (Allman, 1883)

Inhaca, Barreira Vermelha: infertile stems reaching 13 mm.

Inhaca Est (dragage): two infertile stems reaching 6 mm.

Inhaca, Ponta Torres: a fertile colony reaching 14 mm.

†**Aglaophenia cupressina* Lamouroux, 1816

Santa Carolina: several fertile colonies reaching 260 mm.

Gymnangium gracilicaule gracilicaule (Jäderholm, 1903)

Inhaca, Station: an infertile colony reaching 94 mm.

**Gymnangium gracilicaule lignosum* (Millard, 1968)

Santa Carolina: several infertile stems reaching 35 mm.

Lytocarpus philippinus (Kirchenpauer, 1872)

Inhaca, Station: infertile colonies reaching 41 mm, on weed.

Ihla dos Portugueses: one infertile stem of 104 mm.

Inhaca, Saco: luxurious infertile stems reaching 147 mm.

Inhaca, Ponta Torres: luxurious infertile stems reaching 112 mm.

Santa Carolina: infertile fragments and young colonies.

†*Thecocarpus delicatulus* (Busk, 1852)

Santa Carolina: infertile stems reaching 30 mm.

Family **Proboscidae**†**Proboscidae* (*Lar*) sp.

Inhaca, Barreira Vermelha: five colonies, one fertile.

SYSTEMATIC SECTION

Family **Tubulariidae***Ectopleura bethae* (Warren, 1908)

Tubularia betheris Warren, 1908: 280; pl. 45, figs 10, 11; pl. 46, fig. 12.

Description

A colony of many individuals reaching a maximum height of 30 mm. Perisarc smooth or irregularly annulated in some areas, stiff to about 0,5 mm below hydranth body, then becoming thin and membranous and terminating on the basal dilation. Mature hydranth about 1,5 mm in height to tip of hypostome, with up to 15 aboral tentacles and 17 oral tentacles. Aboral tentacles reaching 1,8 mm, oral tentacles reaching 0,5 mm.

In the young hydranth the oral tentacles are definitely capitate with a terminal battery of nematocysts. In the mature one the capituli are no longer distinct but there is still a concentration of nematocysts on the distal end. The smallest hydranth present is 0,42 mm in height and has nine filiform aboral tentacles 0,24 mm long, and nine capitate oral tentacles 0,07 mm long.

Medusa-buds borne on branching blastostyles just above the aboral tentacles, the largest 0,24 mm in height and 0,23 mm in diameter, with four capitate

marginal tentacles 0,06 mm in length and eight exumbrellar bands of nematocysts. In all of them the hypostome is large and fills the umbrellar cavity, and in a few it protrudes through the mouth aperture. It has a circle of nematocysts around the rim.

Remarks

This species resembles *Ectopleura dumortierii* (Van Beneden) in the presence of four medusa tentacles, but differs from it in the smaller number of hydranth tentacles and in the capitate tentacles of the young hydranth.

Family Cladocorynidae

Cladocoryne floccosa Rotch, 1871

Fig. 1 D, E

Cladocoryne floccosa: Warren, 1908: 284. Behner, 1914: 419, figs 19–23. Philbert, 1936: 1, figs 1–8. Weill, 1937: 1, figs 1–4. Vervoort, 1941: 190. Brinckmann-Voss, 1970: 69, figs 80–82.

Description

Stems unbranched or rarely with one lateral branch, reaching a maximum height of 5,0 mm. Perisarc smooth, or annulated in basal region only. Hydranths with 4–7 oral tentacles and up to 18 branched aboral tentacles.

Male gonophores borne on hydranths amongst the aboral tentacles, these hydranths showing no signs of regression to gonozooids as described by Behner. Gonophores spherical, reaching 0,34 mm in diameter.

Nematocysts of three types:

- (i) Macrobasic euryteles, found on body of hydranth only (Fig. 1 E). Capsule bean-shaped, $28,8\text{--}31,2 \times 11,7\text{--}15,0 \mu$. Butt in two sections, the first unarmed, the second armed with spiral bands of fine spines and increasing slightly in width distally. Thread unarmed.
- (ii) Large stenoteles, found in capitula of tentacles. Capsule oval, $12,6\text{--}14,4 \times 10,8\text{--}12,0 \mu$. Details of armature not distinguishable.
- (iii) ?Small stenoteles, abundant in capitula of tentacles and also present on hydranth body. Capsule oval, $6,0\text{--}6,7 \times 5,0\text{--}5,7 \mu$. Not seen discharged.

Remarks

The nematocysts of this material agree with those described by Philbert & Weill, except that the two categories of stenoteles are smaller. Warren's 'large' and 'small' nematocysts appear to correspond to the large and small stenoteles respectively.

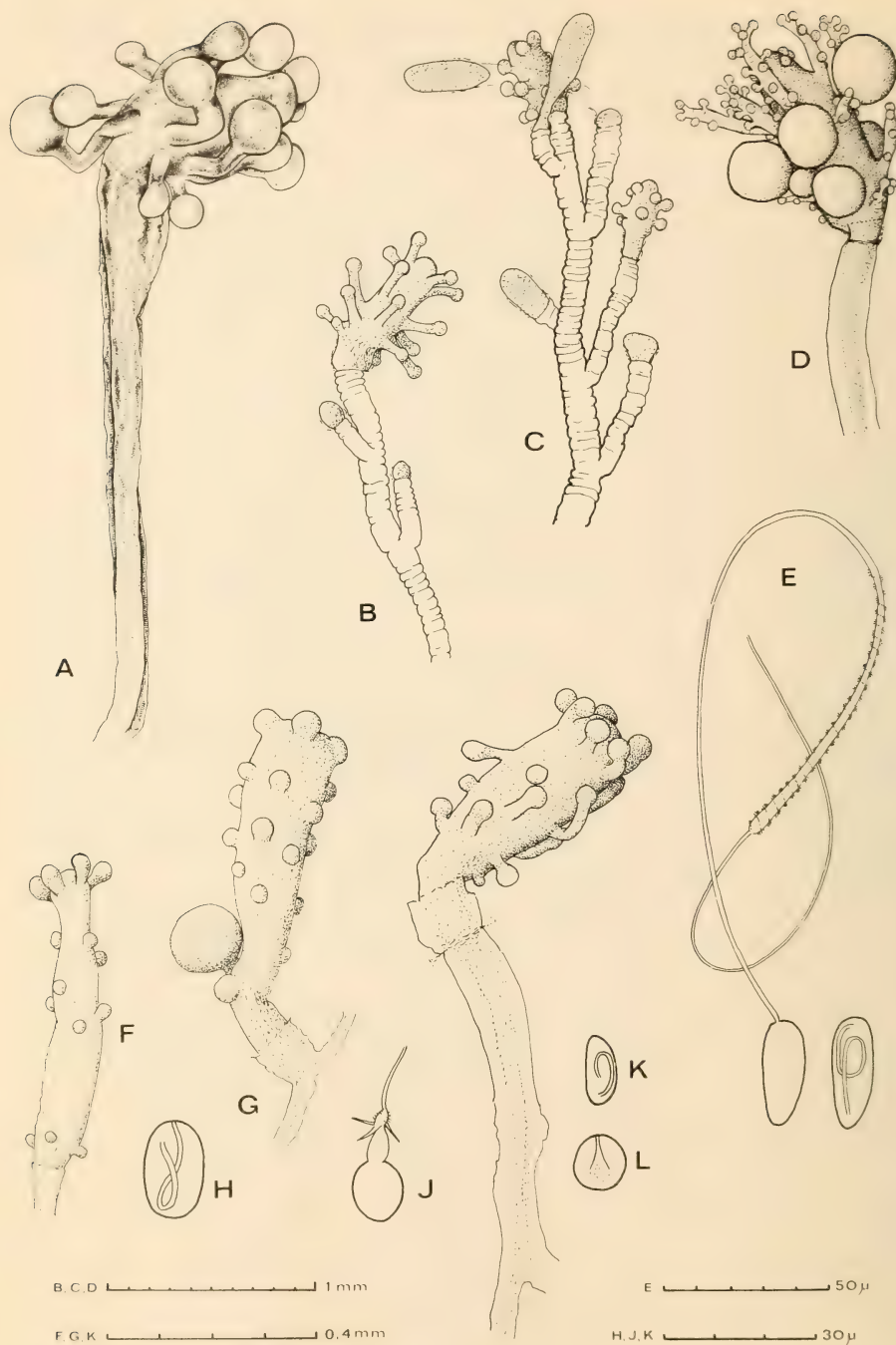


Fig. 1.

A. *Sphaerocoryne bedoti*. B-C. *Coryne* ?*pusilla*, C showing production of regeneration bodies. D-E. *Cladocoryne floccosa*. D, hydranth with male gonophores, and E, discharged and undischarged macrobasic euryteles. F-L. *Zanclea* sp. F and G, hydranths from colony commensal with polyzoan; H and J, large bean-shaped nematocyst and large stenotele from the same colony; K, hydranth from colony commensal with coral; L, small bean-shaped nematocyst and large stenotele from the same colony.

Family *Corynidae**Coryne ?pusilla* Gärtner, 1774

Fig. 1 B, C

Coryne pusilla: Hincks, 1868: 39; pl. 7, fig. 1. Warren, 1908: 289, fig. 4.*Description*

Stems unbranched or with a few lateral branches, reaching about 4 mm in height. Stem closely annulated throughout or with the basal part only roughly corrugated; perisarc continued over the base of the hydranth as far as the first tentacles as a very thin transparent membrane, but not expanded in any way.

Hydranths 0,37–0,75 mm in length and about 0,2 mm in maximum diameter. Tentacles 11–19 in number, 3–5 forming a verticil round the mouth and the remainder irregularly scattered or with a tendency to form 3–4 alternating verticils.

Nematocysts: stenoteles of varying size, $8,4 \times 4,8$ – $15,0 \times 9,0$ μ .

Remarks

It is impossible to be certain about the identity of this material in the absence of gonophores. Warren has reported *C. pusilla* from Natal, and the annulation of the stem suggests this species. The dimensions and number of tentacles of the hydranth agree with Warren's 'dwarf form', which, however, was sterile and thus its identity subject to doubt. The continuation of the perisarc over the base of the hydranth resembles the condition illustrated by Prévot for *C. fucicola* (1959: fig. 7) but it is not swollen or expanded as is the case in *C. muscoides*.

Some of the specimens show vigorous asexual reproduction, the tips of lateral branches becoming separated off as regeneration bodies (Fig. 1 C). These bodies (frustules), when completely separate, are very similar to planula larvae, containing an outer layer of columnar ectoderm and an inner solid layer of endoderm. They measure 0,41–0,53 mm in length and 0,13–0,18 mm in diameter.

Sphaerocoryne bedoti Pictet, 1893

Fig. 1A

Sphaerocoryne bedoti Pictet, 1893: 10; pl. 1, figs 5, 6. Mammen, 1963: 48, figs 16–18.*Clavatella multitentaculata* Warren, 1908: 278; pl. 45, figs 7–9.*Sphaerocoryne multitentaculata*: Stechow, 1921: 248. Prévot, 1959: 108. Gravier, 1970: 149.*Description*

Pedicel (possibly incomplete) and hydranth together reaching a total height of 3,5 mm. Pedicel increasing in diameter distally, 0,11 mm wide at base, 0,16 mm

at distal end; perisarc smooth. Hydranth body 0,7 mm in length (preserved), with 15 capitate tentacles in two alternating verticils.

Remarks

This is probably a young hydranth.

Family *Zancleidae*

Zanclea sp.

Fig. 1 F-L

Description

Four commensal zancleid colonies have been collected in the Inhaca area, all of which superficially appear to fall within the range of *Z. costata*, as discussed by Millard & Bouillon (1973). However, the first of these shows certain differences in host and cnidome from the other three, and will be described separately.

Colony 1: (Fig. 1 K, L)

Colony commensal with a coral. Hydrorhiza coated with firm perisarc and ramifying on the surface of the coral skeleton below the soft body. Hydrocaulus penetrating the coral body and emerging at the surface through a pore, enclosed in perisarc to just above level of emergence where it becomes membranous and creased.

Hydranths all infertile, reaching a maximum height of 1,1 mm, with 18-28 stalked capitate tentacles, of which six form an oral whorl and the rest are irregularly scattered.

No large bean-shaped nematocysts comparable with those of the Seychelles colonies could be found, but a very few small bean-shaped capsules measuring $13,8 \times 6,0 \mu$ were seen in the lower part of the body.

Large and small stenoteles, measuring $10,8 \times 9,0 \mu$ and $6,0 \times 4,8 \mu$ respectively, occur abundantly in the tentacles and the body.

Colonies 2, 3 and 4 (Fig. 1 F-J)

Colonies commensal with polyzoa. Hydrorhiza ramifying within the polyzoan and coated with thin perisarc which terminates at the level of emergence of the hydrocaulus or slightly above.

Hydranths reaching a maximum height of 0,8 mm, with 11-24 tentacles, of which 3-5 have larger capitulae than the rest and form an oral whorl, and the remainder are irregularly distributed over the body. Tentacles mostly with very short stalks and some reduced to mere knobs.

Medusa-buds borne on the lower part of the hydranth either amongst the lower tentacles or below them, 1-3 per hydranth. Largest medusa 0,16 mm in diameter and showing rudiments of marginal bulbs.

Nematocysts of three types:

- (i) Large, bean-shaped capsules, probably macrobasic euryteles, varying slightly in shape from $19,2 \times 10,8 \mu$ to $22,8 \times 7,8 \mu$. Butt forming at least one loop in the longitudinal axis. Present in body and hydrocaulus.
- (ii) Large stenoteles with almost spherical capsules, reaching $11,4 \times 10,8 \mu$, present in capitulae of tentacles and elsewhere in the body.
- (iii) Small stenoteles with almost spherical capsules, $6,0 \times 4,8 \mu$, abundant in tentacles and also present elsewhere in body.

These colonies show shortening of the tentacles which may be concomitant with the early reproductive stage. The appearance of the undischarged capsules of the large bean-shaped nematocysts is slightly different from those of the Seychelles material described by Millard & Bouillon (1973).

Family Clavidae

Rhizogeton nudum Broch, 1909

Fig. 2A

Rhizogeton nudum Broch, 1909: 137, fig. 1. Ritchie, 1910: 827, fig. 80. Mammen, 1963: 34, fig. 3. Rees & Thursfield, 1965: 48.

Description

Hydrorhiza reticular, coated with a transparent layer of perisarc. Hydranths sessile, cylindrical, 0,84–2,00 mm in height, with a very low collar of perisarc around the base, with 16–26 filiform tentacles scattered over the distal two-thirds of the body and increasing in length distally so that the most distal are about three times the length of the most proximal.

Gonophores male, borne directly on hydrorhiza, oval, completely enveloped in thin perisarc, reaching a maximum size of $0,29 \times 0,23$ mm.

Remarks

This species was originally described from the Arctic and has since been reported from the same area several times by Kramp (1932, 1943). Infertile material has been reported from the Pacific Ocean (Ritchie 1910) and from India (Mammen 1963). The presence of male gonophores similar to those of Broch in the present material seems to confirm the presence of the species in the Indian Ocean in spite of the peculiar discontinuity of the distribution.

Turritopsis nutricula McCrady, 1856

Turritopsis nutricula: Russell, 1953: 115, figs 54–56; pl. 5, figs 1–5; pl. 29, figs 1–3. Vervoort, 1968: 5. Millard & Bouillon, 1973: fig. 4C.

Description

Larger stems reaching 5 mm in height, branching irregularly, but unfascicled and presumably still young. Perisarc of stem in two layers, the inner firm and

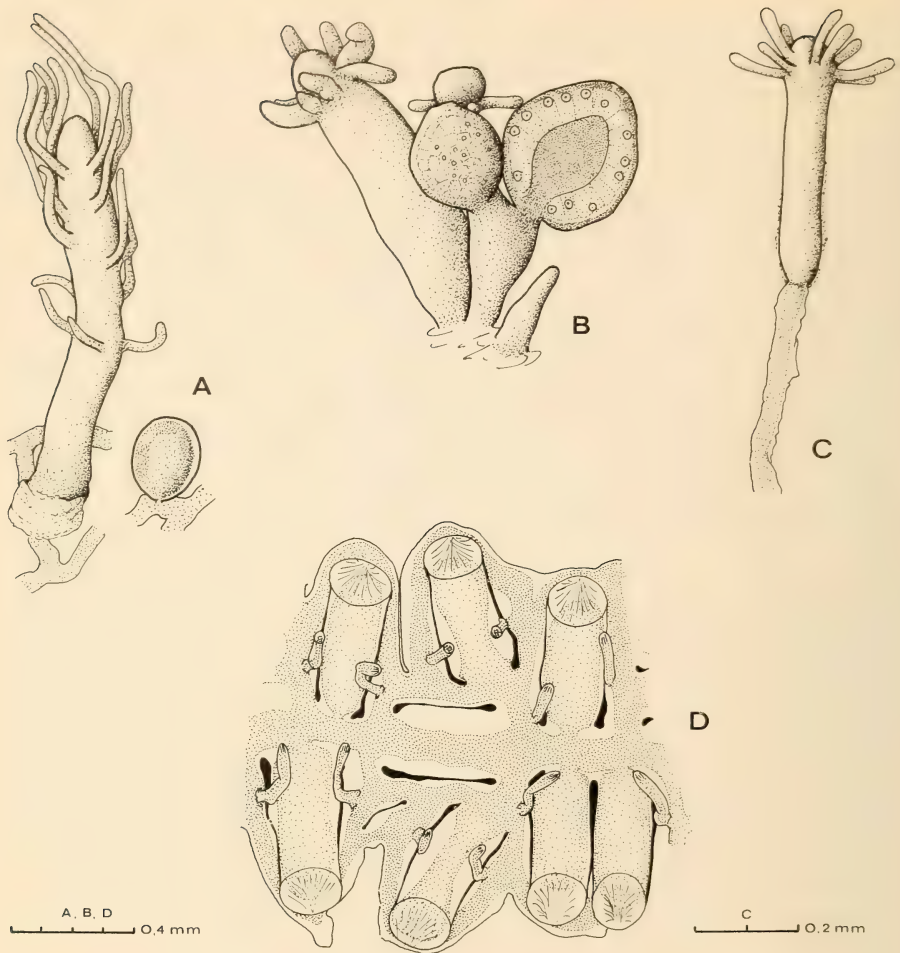


Fig. 2.

A. *Rhizogeton nudum*, hydranth and male gonophore. B. *Podocoryne ?carnea*, gastrozoid, gonozooid and spine. The right gonophore is shown in half section. C. *Incertae sedis* species 1. D. *Lineolaria* sp., surface view of colony with hydrothecae and nematothecae.

corrugated, the outer thin and sometimes with adhering silt. Branches adnate and parallel to stem for some distance, then diverging at an acute angle. Several young and unbranched stems present bearing a single terminal hydranth, only slightly more advanced than those illustrated by Russell (1953: pl. 5, fig. 5); the perisarc in these also in two layers.

Hydranth with 12–38 scattered filiform tentacles, the proximal ones shorter than the distal.

Young medusa-buds borne below hydranths on the taller stems, about 0,10 mm in diameter.

Family **Eudendriidae***Eudendrium capillare* Alder, 1856

Fig. 3 E-H

Eudendrium capillare Alder, 1856: 355; pl. 12, figs 9-12. Picard, 1955: 183. Mammen, 1963: 57, figs 25, 26.

Eudendrium parvum Warren, 1908: 272, fig. 1; pl. 45, figs 1-4.

Eudendrium ?parvum: Millard, 1959: 305, fig. 1 G-H.

Non Eudendrium ?capillare: Millard, 1966: 454.

Description

Stem unfascicled, unbranched or sparsely and irregularly branched, reaching 1,4 cm in height, annulated or corrugated on origins of branches, hydranth pedicels often annulated or corrugated throughout. Hydranth with 17-23 tentacles (mean number 19 in eight counts).

Male gonophores present in two colonies, one- to three-chambered, sometimes with a terminal tubercle, borne on completely atrophied hydranths—even in the youngest there is no sign of tentacles.

Female gonophores present in two colonies; young ones borne by partly atrophied hydranths in which tentacles are present but reduced in size, spadix unbranched; one old blastostyle present in which the tentacles are completely absent and the spadices of the gonophores shed. Eggs orange in colour, reaching 0,22 mm in diameter.

Only small nematocysts present, abundant on tentacles and also present in hydranth body: microbasic euryteles, $6,6 \times 2,4-8,0 \times 3,0 \mu$, undischarged only.

Remarks

This is the first of three small species of *Eudendrium* which occur at Inhaca. They are all very similar in their growth-form and all have female gonophores with an unbranched spadix. As Picard (1951, 1955) has shown, the only sure way of distinguishing such species is by nematocyst structure. *E. capillare* differs from the other two in the complete absence of large nematocysts. It also differs in the absence of tentacles at all stages of development of the male blastostyles.

Eudendrium motzkossowskiae Picard, 1951

Fig. 3 J, K

Eudendrium simplex: Motzkossowska, 1905: 56; pl. 3, figs 18, 19.

Eudendrium motzkossowskiae Picard, 1951: 339.

Description

Stems unfascicled, unbranched or sparsely branched, reaching 1,2 cm in height, smooth for the most part but annulated on origins of branches and at other irregular intervals, hydranth pedicels sometimes annulated or corru-

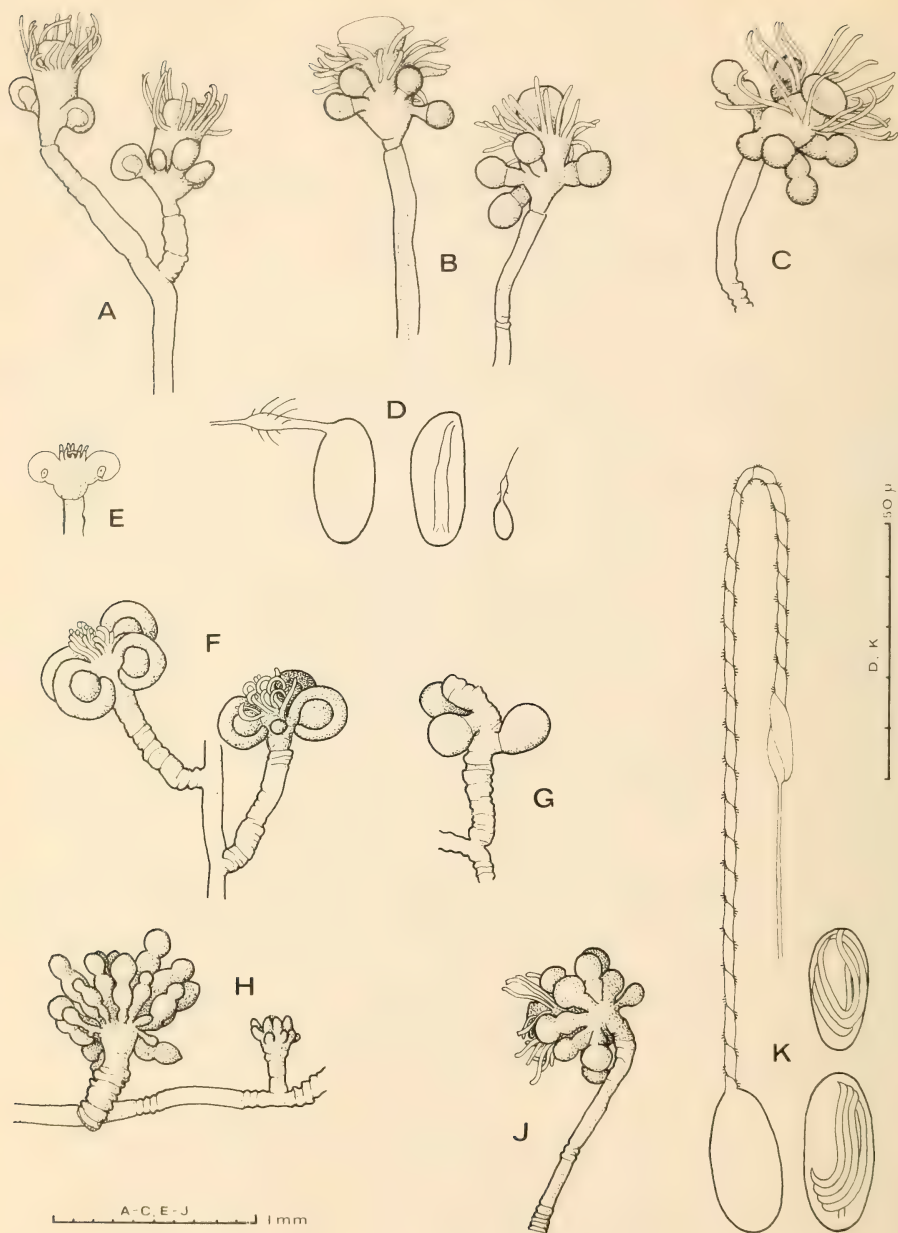


Fig. 3.

A-D. *Eudendrium ramosum*. A, young female blastostyles; B and C, male blastostyles; D, large microbasic eurytele discharged and undischarged and small microbasic eurytele discharged. E-H. *Eudendrium capillare*. E, very young female blastostyle; F, slightly older female blastostyles; G, old female blastostyle with spadix shed; H, old and young male blastostyles. J-K. *Eudendrium motzkossowskiae*. J, male blastostyle; K, large macrobasic eurytele discharged and undischarged.

gated throughout. Hydranth with 16–27 tentacles (mean number 20 in 11 counts).

Male gonophores present in two colonies, one- and two-chambered, borne on non-atrophied hydranths. Female gonophores absent.

Nematocysts of two types:

- (i) Large macrobasic euryteles present on hypostome and lower part of hydranth body; sometimes rather scarce and present on only some hydranths of a colony, at other times abundant. Size rather variable, $15,6 \times 6,0$ – $31,6 \times 14,0$ μ . Undischarged capsule with butt in 3–4 obliquely longitudinal coils. Discharged capsule with butt 5–6 times length of capsule (150–165 μ), swollen distally to about double the width, bearing spirally arranged barbs which appear to be absent on most of the terminal dilation. Thread less than half width of proximal part of butt.
- (ii) Small microbasic euryteles present on tentacles and elsewhere, $6,6 \times 2,4$ – $7,2 \times 3,0$ μ , undischarged only.

Remarks

From the experience of the second author with Mediterranean hydroids, the size and structure of the large nematocysts in this material indicate an identity with *E. motzkossowskiae*, so far known only from the Mediterranean. The discovery of the characteristic female gonophores with hermaphrodite contents is awaited to completely confirm the diagnosis.

Eudendrium ramosum (Linnaeus, 1758)

Fig. 3 A–D

Eudendrium ramosum: Allman, 1872: 332; pl. 13. Leloup, 1952: 127, fig. 64. Picard, 1955: 183. Millard, 1966: 456. Millard & Bouillon, 1973: 32, fig. 4F.

Description

Stem unfascicled, unbranched or sparingly branched with an alternate tendency; almost entirely smooth both on main stem and pedicels except for groups of a few annulations on origins of branches and at other rare intervals, reaching 2,0 cm in height. Hydranths with 18–29 tentacles (mean number 23 in 36 counts).

Male gonophores present in five colonies; one- or two-chambered, borne on non-atrophied hydranths. Female gonophores present in five colonies, borne on non-atrophied hydranths, with unbranched spadix.

Nematocysts of two types:

- (i) Large microbasic euryteles, present on hypostome and lower part of hydranth body, on spadix of female gonophore and on distal end of male gonophore, $22,5 \times 10,5$ – $28,8 \times 13,8$ μ . Undischarged capsule with butt about three-quarters length of capsule (0,67–0,84), increasing distally to about twice the diameter. Discharged capsule with butt

about three-quarters length of capsule and extruded at right angles to its main axis, dilated distally to about twice the diameter. Armature not clearly observed. Occasionally absent in some hydranths of a colony.

- (ii) Small microbasic euryteles, present on tentacles and elsewhere, $6,6 \times 2,4$ – $8,4 \times 4,2$ μ . Discharged capsule with butt about three-quarters length of capsule, dilated in distal half, armature not clearly observed.

Remarks

This is by far the most common of the three species of *Eudendrium*. It is surprising that all the colonies are so small and that none has a fascicled stem. However, larger colonies reaching 17,5 cm have been reported from the Cape, South Africa (Millard 1966).

Family Hydractiniidae

Hydractinia diogenes Millard, 1959

Hydractinia diogenes Millard, 1959: 305, fig. 2.

Description

Colonies very similar to holotype. Spines rather scarce, reaching 0,5 mm in length. Gastrozooids reaching 2,9 mm in height and with 10–16 tentacles. Gonozooids reaching 1,2 mm in height and with up to nine tentacles. Gonophores, all female, of various sizes, the largest 0,45 mm in depth and 0,47 mm in diameter.

Spiral zooids present on edge of one colony, reaching a length of 2,6 mm and bearing a terminal battery of nematocysts.

Podocoryne ?carnea M. Sars, 1846

Fig. 2B

Hydractinia carnea: Millard, 1957: 181.

Podocoryne carnea: Edwards, 1972: 122, 136, figs 7–9.

Description

Hydrorhiza forming an open meshwork in younger parts and an incrustation of coalesced tubes in the older parts. Spines hollow, transparent or horn-coloured, straight or curved, about 0,3 mm in height. No spiral zooids or tentaculozooids.

Gastrozooids reaching 1,14 mm in height (preserved), with 7–10 tentacles, usually long and short alternating. No perisarcial cup round base.

Gonozooids more slender than gastrozooids and often much smaller,

reaching 1,14 mm in height (preserved), with 4–7 tentacles, bearing 1–3 gonophores on lower half.

Gonophores packed with about 60 eggs in seven or eight tiers, the largest gonophore $0,57 \times 0,49$ mm, with four radial canals and a circular canal, and in some, rudiments of four marginal bulbs or tentacles.

Remarks

These gonophores are very similar to those with precociously developed sexual products in material ascribed to *P. carnea* by Millard & Bouillon (1973), and by Millard (1957). They differ in the larger number of smaller eggs.

Several other infertile hydractiniids on various substrata, including barnacles, worm-tubes, empty gastropod shells and a *Pecten* shell, may possibly be the same species. Some possess spines and others are without. Some possess spiral zooids scattered amongst the hydranths.

INCERTAE SEDIS

Species 1

Fig. 2C

Description

Hydrocaulus unbranched, perisarc firm and roughly corrugated in lower part but increasing in diameter and becoming very thin distally to continue over the body of the hydranth as a membranous layer, terminating below the tentacles.

Hydranth minute, cylindrical, fairly clearly demarcated from hydrocaulus, with conical hypostome and a single whorl of 7–9 filiform tentacles held alternately elevated and depressed, no web between the tentacles. Hydranth 0,17–0,48 mm in length. Total height (hydranth plus hydrocaulus): 0,62–1,16 mm.

Remarks

These specimens show some resemblance to hydranths of the family Pandeidae, and especially to the genus *Amphinema*. They resemble *A. rugosum* in the corrugated perisarc and *A. dinema* in the membranous terminal part of the perisarc. It is not possible to be more definite in the absence of gonophores.

Species 2

Description

A stolonial colony with reticular hydrorhiza creeping among sand grains and giving rise to solitary hydranths. Hydrorhiza and hydrocaulus enclosed in perisarc. Hydranth emerging from side of hydrocaulus, with 10–13 filiform tentacles, reaching a maximum height of 0,64 mm when extended. Hydrocaulus reaching a height of 2,55 mm.

Remarks

This is the same species described by Millard & Bouillon (1973: fig. 4H). The hydrocaulus is taller in this material, but shows no indication of branching. The systematic position remains uncertain.

Species 3

Lineolaria sp.

Fig. 2D

Lineolaria sp. Gravier, 1970: 144, figs 11, 13A. Gravier, 1972: 8.

Description

Colony growing on *Cymodocea*. Hydrorhiza generally running parallel to the long axis of the frond, in single, double or triple strands connected to one another by cross anastomoses; each longitudinal strand giving rise to a row of hydrothecae on each side which may be alternate, opposite or irregular.

Hydrotheca tubular, adherent to weed for most of its length, then bent upwards. Perisarc thickened near base, becoming thin distally. Margin facing obliquely upwards, circular, untoothed, with an operculum of many delicate converging segments. Hydranth with about 14 tentacles and a conical hypostome.

Nematothecae borne on hydrorhiza on the transverse connections, one or two flanking each hydrotheca and leaning over it, erect, not adherent, tubular, containing a group of large nematocysts.

Gonothecae absent.

Measurements (mm)

Hydrotheca, length	0,42-0,57
diameter at margin	0,16-0,21
Nematotheca, length	0,15-0,22
maximum diameter	0,04-0,05

Remarks

This appears to be the same species as that briefly described and illustrated by Gravier from Madagascar. We have refrained from naming the species or placing it in a family pending a forthcoming publication by Gravier.

Family **Haleciidae***Halecium tenellum* Hincks, 1861

Halecium tenellum: Vervoort, 1959: 229, fig. 8. Millard, 1966: 471, fig. 11 C-F.

Description

This small species occurs abundantly on any available substratum. Some of the stems are beautifully regular and geniculate, with a hydrotheca arising from

each internode. Others are less regular, with numbers of intervening athecate internodes, particularly in the basal region. Branches arise singly or in pairs from the distal ends of the internodes. Rejuvenation is common and many tiers of secondary hydrothecae occur.

Male and female gonothecae occur on separate colonies and arise either from the hydrorhiza or from the upright stem. They are similar to those previously described (Millard 1966).

Hydrodendron gardineri (Jarvis, 1922)

Fig. 4

Halecium gardineri Jarvis, 1922: 334; pl. 24, fig. 1.

Description

Hydrorhiza reticular and strengthened by internal thickenings of perisarc, giving rise to solitary hydrophores and erect stems. Stem reaching a maximum height of 4 mm, unfascicled, unbranched, divided into internodes by oblique nodes sloping in alternate directions. Each internode bearing a single hydrophore on a short apophysis arising near the centre or at about two-thirds of the length. Hydrophores alternate, the two rows in one plane.

Hydrophore (Fig. 4B) consisting of a pedicel separated from the apophysis by a twisted node, bulging slightly at base, then expanding smoothly to merge into the cup-shaped hydrotheca; completely symmetrical or with an oblique margin. Hydrotheca deep, with oblique diaphragm sloping downwards on adcauline side; margin not, or slightly, everted; marginal diameter approximately equal to depth on adcauline side. Many hydrophores regenerated, resulting in supplementary internodes, which are often roughly corrugated, between the apophysis and the pedicel (Fig. 4A). Solitary hydrophores usually with a number of supplementary internodes at base (Fig. 4C and D). No refringent nodules in hydrotheca.

Nematothecae borne irregularly on hydrorhiza, on stem and on regeneration nodes, but none seen on unregenerated pedicels, goblet-shaped, with everted margin. Nematophore with a solid core of endoderm cells and a terminal capitulum.

Hydranth with 18 tentacles in the only expanded example, and no inter-tentacular web, large but apparently just able to be contained in the hydrotheca.

Nematocysts of at least two types (Fig. 4G):

- (i) Small microbasic mastigophores, abundant on tentacles. Capsule $5,4 \times 1,8 \mu$ (discharged). Butt $4,8 \mu$ in length, with about six spiral bands of short spines.
- (ii) Large heteronemes, seen on nematophores only, $18,0 \times 6,6 \mu$ (undischarged).

Gonophores absent.

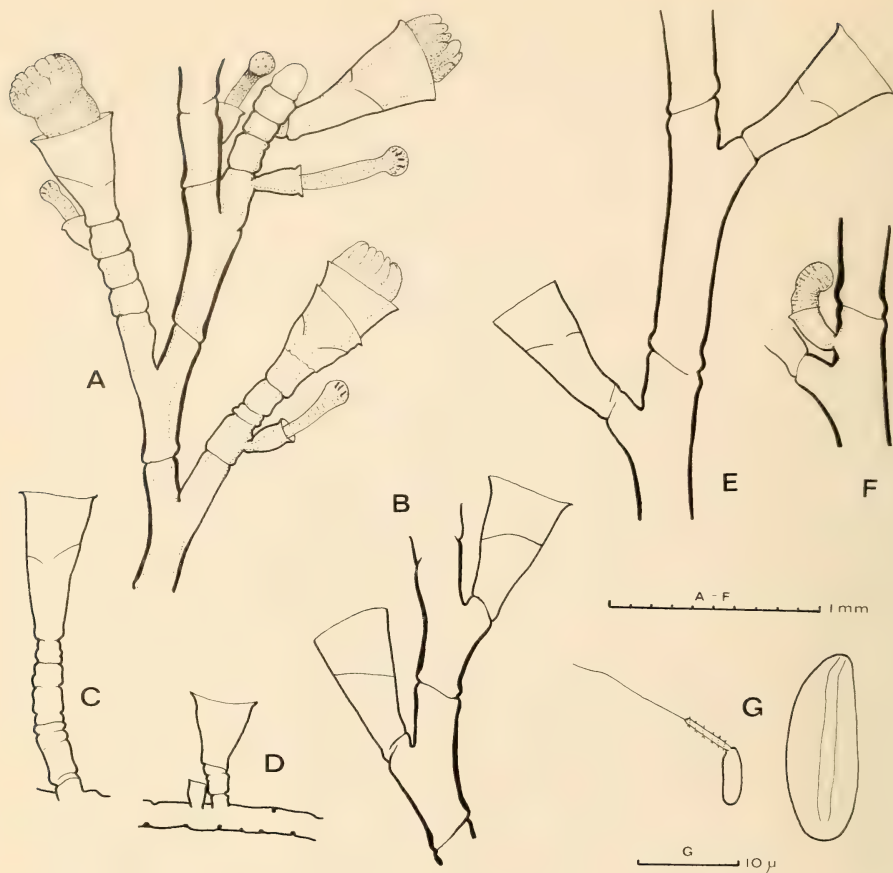


Fig. 4. *Hydrodendron gardineri*.

A-B. Parts of erect stem showing hydrophores and nematophores. C-D. Solitary hydrophores, D with a nematotheca. E-F. Parts of an erect stem from Jarvis's schizotype. G. Macrobasic mastigophore and large heteroneme.

Measurements (mm)

Stem, internode length	0,18-0,34
diameter across node	0,06-0,09
Hydrophore, length adcauline, unregenerated	0,20-0,23
Hydrotheca, depth adcauline	0,11-0,16
diameter at margin	0,13-0,17
Nematotheca, depth	0,08-0,10
diameter at margin	0,05-0,07

Jarvis's type

0,30-0,50
0,08-0,10
0,24-0,30
0,11-0,14
0,14-0,17
0,08-0,09
0,05

Remarks

Through the courtesy of the British Museum (Natural History) we were able to examine a prepared slide of Jarvis's type material of *Halecium gardineri*

(Fig. 4 E and F: schizotype, no. 23.2.15.9) from Chagos and there is no doubt about the identity of the Inhaca material. Measurements from the type are included above as none were given by Jarvis and her quoted magnification is not accurate.

Hydrodendron sympodiformis n. sp.

Fig. 5

Holotype: a very rich fertile colony on weed from Inhaca, Ponta Torres.

Description

Hydrorhiza creeping, branching and reticular, with internal thickenings of perisarc in some areas only.

Hydrophores arising from hydrorhiza, either unbranched and solitary or branching in a very obviously sympodial manner to reach a maximum height of 7 mm. Solitary hydrophores pedicellate, with pedicel of variable length widening distally to merge into hydrotheca. Shorter pedicels completely smooth, longer ones (possibly regenerated) with one or two nodes or corrugations near base. In branching stems each hydrophore giving off a lateral apophysis near distal end which bears the next hydrophore, this process being repeated up to nine times, the base of each hydrophore being curved upwards so that it stands almost parallel to the preceding one; the series of apophyses not in one plane but arising from any surface. Two apophyses sometimes arising at the same level, so producing a dichotomous appearance.

Hydrotheca widening to margin, which may or may not be everted, with diameter usually a little over twice the depth, with a straight diaphragm and a circle of refringent nodules between margin and diaphragm. Hydranth with about 22 tentacles.

Nematothecae borne in random fashion on hydrorhiza and hydrophore pedicels, vase-shaped, with an everted margin and a perisarc thickening just below it. Nematophore with a solid core of endoderm cells and a terminal capitulum containing a battery of large nematocysts about $22,5 \times 10 \mu$.

Gonothecae borne in abundance on hydrorhiza, all female, barrel-shaped but with widest part below centre, with 6–7 very distinct transverse annulations and a terminal aperture on a narrowed neck, containing one planula larva.

Measurements (mm)

Hydrotheca, depth, margin to diaphragm	0,06–0,10
diameter at margin	0,17–0,22
Nematotheca, depth	0,14–0,20
diameter at margin	0,09–0,11
Gonotheca, depth	0,63–0,80
maximum diameter	0,39–0,44
diameter at margin	0,20–0,26

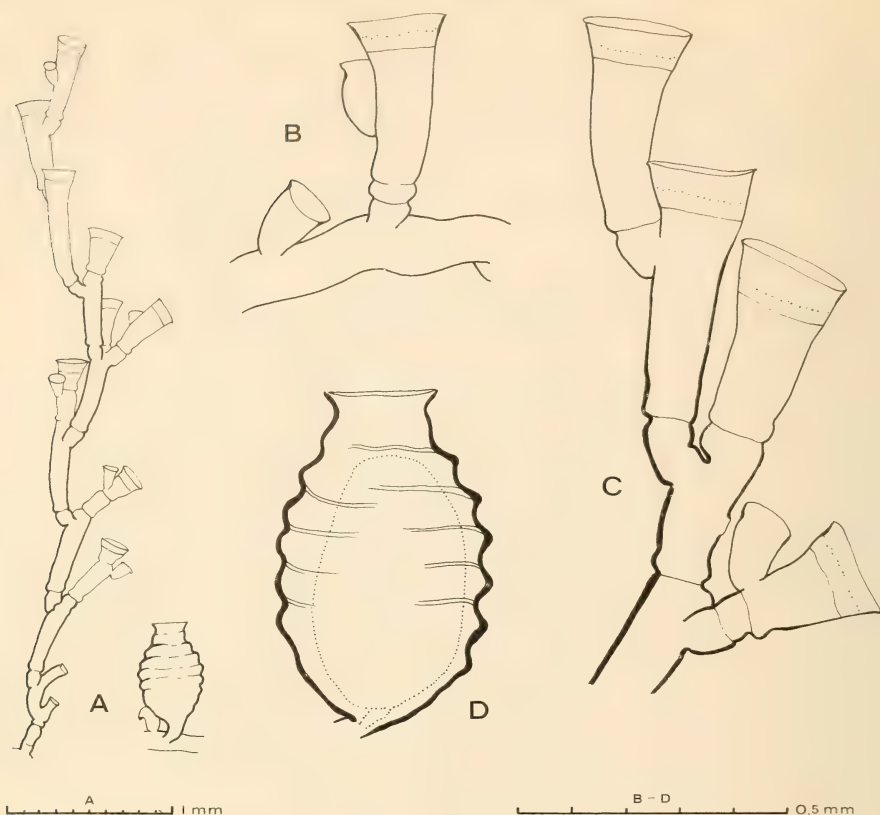


Fig. 5. *Hydrodendron sympodiiformis* n. sp.

A. Complete stem and gonotheca. B. Solitary hydrophore and nematotheca. C. Part of stem. D. Gonotheca.

Remarks

The growth-form of this material shows similarities to that of *H. negligens* (Fraser 1938) and *H. alternata* (Fraser 1938) from the Pacific, but certain differences from the structure of the trophosome of both and from the shape of the gonotheca in the latter seem to merit the establishment of a new species.

Family Campanulariidae

Campanularia delicata (Trebilcock, 1928)

Orthopyxis delicata Trebilcock, 1928: 3; pl. 2, fig. 1. Ralph, 1957: 837, 840, fig. 7 a-d.

Campanularia delicata: Millard & Bouillon, 1973, fig. 6 G-M.

Remarks

The hydrothecae and gonothecae (male) of this material are similar to those described by Millard & Bouillon (1973), from the Seychelles and show similar variations. The hydrothecal pedicels in particular show much variation in length and amount of annulation.

Clytia sp.

Fig. 6A

Description

Colony stolonial. Pedicel closely annulated at base and distal end. Hydrotheca deep and slender, with height $2\frac{1}{4}$ – $3\frac{1}{2}$ times diameter, margin with 5–8 triangular, slightly asymmetrical teeth. Diaphragm well developed.

Measurements (mm)

Pedicel, height	0,44–1,12
Hydrotheca, depth	0,48–0,59
diameter at margin	0,14–0,24

Remarks

The hydrothecae have the same proportions as *C. warreni* Stechow, 1919, from South Africa, *C. elongata* Marktanner-Turneretscher, 1890, from New Zealand, and *C. ulva* Stechow, 1919, from Marseille. They differ from *C. elongata* in the deeper marginal teeth. The actual size is intermediate between that of *C. ulvae* and *C. warreni*. The marginal teeth are fewer in number than any of the three species mentioned.

In the absence of gonothecae and because of the small size of the sample it is not possible to diagnose the material with any certainty. It might possibly be an extreme variation of *C. hemisphaerica*.

Family **Lafoeidae***Scandia mutabilis* (Ritchie, 1907)*Description*

Hydrothecal pedicels very variable in length, 0,3–4,2 mm, but always annulated. Hydrothecae also variable in size, 1,6–3,9 mm in height, generally quite smooth, but a few with very faint transverse corrugations.

Family **Sertulariidae***Abietinaria laevimarginata* (Ritchie, 1907)

Fig. 7 A–C, E–H

Sertularia laevimarginata Ritchie, 1907: 507; pl. 26, figs 5, 6.*Sertularia linealis* Warren, 1908: 308, fig. 9. Millard, 1958: 195, fig. 8 D, G.*Abietinaria laevimarginata*: Stechow, 1921: 258. Gravier, 1972: 8, fig. 2C.*Non Sertularia linealis* var. *longa* Millard, 1958: 197, fig. 8E. Millard & Bouillon, 1973, fig. 9 E, F.*Non Sertularia linealis*: Millard, 1968: 272.*Description*

Hydrorhiza creeping on weed and typically forming longitudinal lines with cross-connections; with no regular internal pegs of perisarc, but usually

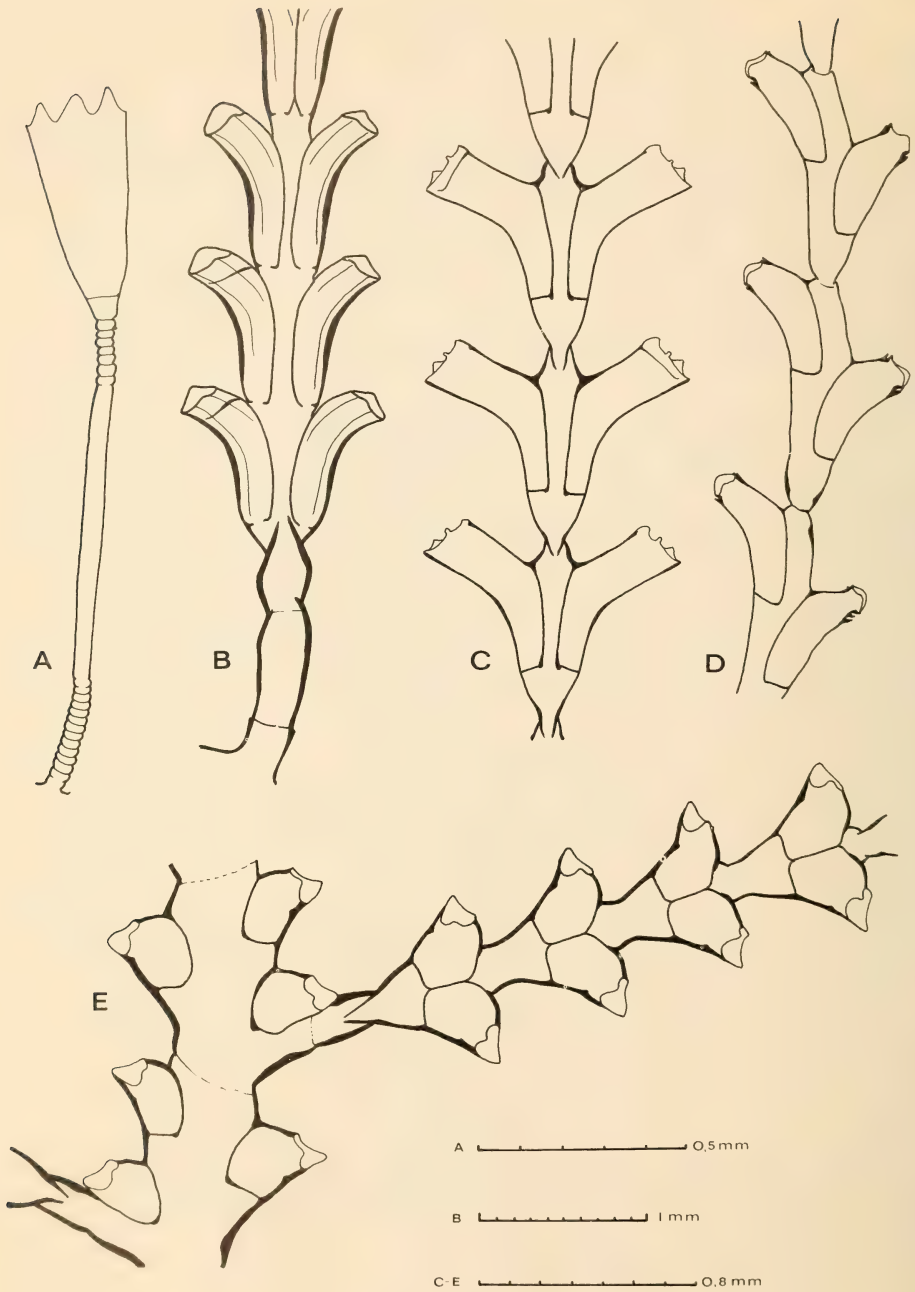


Fig. 6.

A. *Clytia* sp. B. *Diphasia digitalis*, unbranched stem. C. *Diphasia tetraglochina*, unbranched stem. D. *Dynamena crisioides*, var. *alternata*, hydrocladium. E. *Sertularia marginata*, part of stem and hydrocladium.

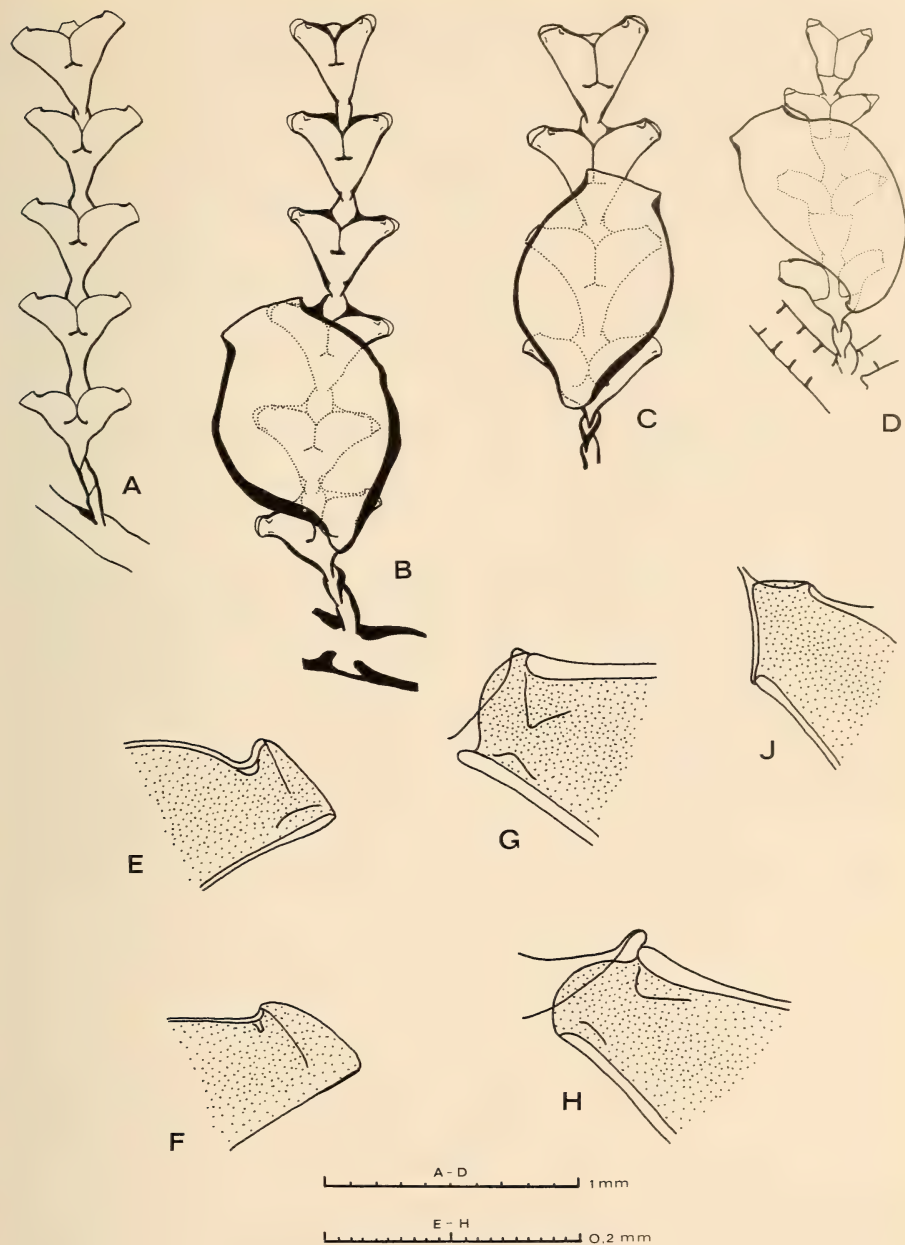


Fig. 7.

A, E-F. *Sertularia laevimarginata* Ritchie, holotype (E and F from different stems). B, G. *Sertularia linealis* Warren, holotype. C, H. *Abietinaria laevimarginata*, from Inhaca. D, J. *Sertularia longa*, from Inhaca. (In E-J the distal part of the hydrotheca is drawn without the near wall to show details of internal teeth and operculum.)

with a group of four ingrowing perisarc lobes around the origin of each stem.

Stem reaching a maximum height of 3,5 mm and bearing a pair of opposite hydrothecae on each internode. Two hinge-joints at the base of each stem, remaining nodes slightly oblique or indistinct.

Hydrotheca bent outwards, narrowing to margin and usually constricted just below it, with thickened perisarc, especially near the adcauline edge. The free adcauline parts of a pair of hydrothecae forming a straight line at right angles to the axis of the stem, except occasionally in the distal pair which are more erect and may subtend an obtuse angle between them. Margin with two low, rounded lateral lobes, which vary considerably in development—they may be quite distinct or almost obsolete. Operculum of one adcauline valve, shed easily. Internal teeth present, including one large adcauline tooth (occasionally double) and two low latero-abcauline teeth.

Gonotheca borne on front of stem below first pair of hydrothecae, smooth, compressed, spherical to ovoid in broad view, with a wide distal aperture on a low collar.

Remarks

Gravier (1972) has synonymized Warren's *Sertularia linealis* with *Abietinaria laevimarginata*. In order to confirm this course of action, and to clarify Warren's statement that *S. linealis* has a 'two-flapped operculum', the first author has examined type material of Warren's *S. linealis* borrowed from the Natal Museum, Pietermaritzburg (No. 747) and from the British Museum of Natural History (Nos. 22.3.6.26, 27 and 33, Fig. 7 B, G). In both these collections whole mounts clearly show a single adcauline opercular valve. But also included in the British Museum material is a slide of sections (No. 22.3.6.32) of a completely different species, with a hydrotheca of a different shape and a two-valved operculum (labelled *S. linealis* but probably *S. distans*). This confusion might thus account for Warren's erroneous statement.

The schizoholotype of *S. laevimarginata* Ritchie (B.M. No. 1964.8.7.148) consists of two infertile stems (Fig. 7 A, E, F). The perisarc throughout is somewhat thinner than in *S. linealis*, and internal thecal teeth are generally absent, though in one hydrotheca three internal teeth are visible, one adcauline and two low latero-abcauline. Around the origin of each stem is one ingrowing lobe of perisarc, not four as in *S. linealis*; however, even in the latter species these lobes are not always conspicuous. The details of shape and dimensions of the hydrothecae are sufficiently like those of *S. linealis* to confirm the synonymy in spite of the minor differences.

With the abundant new material it has now become clear that the first author has previously confused two species under the name of *S. linealis*, due partly to the fact that both have a similar growth-form on weed and may grow together, and to the fact that the hydrothecae of *A. laevimarginata* easily lose the opercula. The second form, described by Millard (1958) as *Sertularia linealis* var. *longa* is now elevated to specific rank (see p. 33 and Fig. 7 D, J). The two

species can be distinguished not only by the form of the operculum, but by differences in the hydrorhiza, presence or absence of internal teeth, and the shape of the gonotheca.

Diphasia digitalis (Busk, 1852)

Fig 6B

Desmoscyphus longitheca Allman, 1877: 26; pl. 14, figs 3-6.

Nigellastrum digitale: Mammen, 1965: 57, fig. 89.

Diphasia digitalis: Vervoort, 1968: 37, fig. 17. Millard & Bouillon, 1973, fig. 9A.

Description

Stems either unbranched, or with alternate branches arising after every two or three pairs of hydrothecae. Branches forming almost a right angle with stem. Hydrothecae in opposite pairs; members of a pair well-separated near the base of the stem, but shifted on to the front and contiguous with one another in the distal parts and on the branches; consecutive pairs close, separated by a distance not more than $\frac{1}{6}$ of their height, but more often in contact or overlapping.

Hydrotheca tubular and curved outwards, usually with three or five longitudinal ridges, in the latter case two anterior, two posterior and one lateral.

Gonothecae absent.

Remarks

The branching of this material is very similar to that figured by Allman (1877) (as *Desmoscyphus longitheca*). In some stems the branches are similarly short, in others they are longer.

The hydrothecae are similar to those described from the Seychelles (Millard & Bouillon 1973), but the longitudinal ridges are more distinct.

Diphasia tetraglochina Billard, 1907

Fig. 6C

Diphasia tetraglochina Billard, 1907: 358, fig. 7. Millard, 1964: 28, fig. 8.

Description

Two of these colonies are exactly similar to the material from the Agulhas Bank, South Africa (Millard 1964), i.e. the hydrothecae are shorter and wider but with a greater proportion adnate ($\frac{2}{3}$ - $\frac{3}{4}$) than those of the type material (Billard 1907).

The third colony, from Cabo da Inhaca (Fig. 6C), is more like Billard's material with taller and more slender hydrothecae with a smaller proportion adnate ($\frac{1}{2}$ - $\frac{2}{3}$).

Measurements of material from Cabo da Inhaca, in mm.

Internode length	0,52-0,63
Hydrotheca, length abcauline	0,40-0,51
length adcauline, adnate part	0,31-0,39
length adcauline, free part	0,18-0,26
adnate part/adcauline length	0,57-0,64
diameter at margin	0,15-0,20

Dynamena crisioides Lamouroux, 1824

Fig. 6 D

Dynamena crisioides: Billard, 1925: 181, figs 36, 37 C-E; pl. 7, fig. 21. Millard, 1958: 183. Mammen, 1965: 51, figs 84, 85.

Dynamena crisioides, var. *peculiaris* Billard, 1925: 185, fig. 38.

Dynamena crisioides, var. *gigantea* Billard, 1925: 186, fig. 37F; pl. 8, fig. 24. Millard, 1958: 183, fig. 6C.

Dynamena crisioides, var. *alternata* Billard, 1925: 187, figs 37G, 39; pl. 7, fig. 22.

Description and remarks

This species is abundant in the collection and shows great variation. The normal variety and Billard's var. *gigantea* both occur and sometimes in the same colony. Possibly the latter is an older stage of the former.

One sample of Billard's var. *alternata* is also present (Fig. 6D), which shows the characters described by Billard, namely two alternate hydrotheca on most of the hydrocladial internodes, hydrothecae less adnate than in the typical form, and hydrocladial apophyses arising below the third hydrotheca of a stem internode instead of below the first as in the typical form. The hydrothecae are smaller than those of the typical form, measuring 0,25-0,33 mm in abcauline length as against 0,34-0,51 mm.

Internal teeth may occur in hydrothecae of any of the three forms, as in Billard's var. *peculiaris*.

Without doubt Mammen is right in his contention that it is not possible to retain separate varieties in this very variable species.

Sertularella

In addition to the single species listed on p. 8, several small specimens of *Sertularella* are present in the collection, but all are infertile and all appear to be juvenile colonies. Since it is not possible to be certain of the form of the adult colony in any of them, no attempt has been made at identification. There appear to be about three species involved.

Sertularia longa (Millard, 1958)

Fig. 7 D and J

Sertularia linealis, var. *longa* Millard, 1958: 197, fig. 8E.*Sertularia linealis*: Millard, 1968: 272.*Sertularia linealis longa*: Millard & Bouillon, 1973, fig. 9 E, F.*Description*

Hydrorhiza creeping on weed and usually forming longitudinal lines with cross-connections; with numerous strengthening internal pegs of perisarc growing in from the sides.

Stem reaching about 3 mm in height and bearing a pair of opposite hydrothecae on each normal internode. An oblique hinge-joint (or rarely two) at the base of each stem and hinge-joints occurring sporadically in the rest of the stem where each one forms the distal termination of a short intermediate athecate internode. Normal nodes slightly oblique.

Hydrotheca bent outwards, and abcauline wall with a definite kink in the lower or middle part, narrowing to margin, with comparatively thin perisarc but thickened around margin. The free adcauline parts of a pair of hydrothecae not forming a straight line, but subtending an obtuse angle between them which becomes smaller near the distal end of the stem where the hydrothecae are more erect. Margin with two well-developed and roundly triangular lateral teeth and sometimes a very low median adcauline one. Operculum of two valves hinged at the adcauline and abcauline edges, the adcauline smaller than the abcauline and divided into two by a median line. No internal teeth.

Remarks

This species has hitherto been confused with *Abietinaria laevimarginata*. See remarks on this species.

Sertularia marginata (Kirchenpauer, 1864)

Fig. 6E

Sertularia marginata: Millard, 1957: 224, fig. 13. Ralph, 1961: 785, fig. 12 a-g. Van Gernerden-Hoogveen, 1965: 39, figs 13-17. Mammen, 1965: 45, fig. 77.*Sertularia inflata*: Vervoort, 1959: 281, figs 39-41. Van Gernerden-Hoogveen, 1965: 45, figs 18-22.*Description*

Pinnate stems, on the whole with very regular segmentation, with few internodes which do not bear the normal hydrocladium and three hydrothecae. Basal athecate part of stem variable in length, 0.7-3.0 mm, terminated by a hinge-joint and containing a variable number of transverse nodes. Between hinge-joint and first hydrocladium 0-2 hydrothecae. Stem geniculate in distal region only. The two rows of hydrocladia in one plane.

Hydrocladium unbranched, separated from basal apophysis by hinge-joint and thereafter divided by very indistinct nodes into thecate internodes. Pairs of hydrothecae more closely set than in the South African material from False Bay (Millard 1957), the interval between consecutive pairs being usually less than, and never more than, the height of the hydrothecae. Hydrothecae also smaller and with less pronounced marginal teeth, 0,15–0,22 mm in abcauline height and 0,09–0,12 mm in marginal diameter.

Remarks

Among recent authors opinions differ as to whether or not *S. marginata* and *S. inflata* should be retained as separate species. Van Gernerden-Hoogveen claims to be able to distinguish between the two in Caribbean material, but the present material, and also that of Mammen (1965) and Ralph (1961), seems to combine features of both. The present authors follow the opinion first expressed by Billard (1925: 178) that *Sertularia marginata*, *S. flosculus*, *S. amplexens*, *S. gracilis*, *S. inflatus* and *S. versluysi* are all synonymous.

Family Plumulariidae

Plumularia obliqua (Johnston, 1847)

Fig. 8 A–D

Plumularia obliqua: Bale, 1884: 138; pl. 12, figs 1–3. Hincks, 1868: 304, fig. 36; pl. 67, fig. 1. Pennycuik, 1959: 180.

?*Monothecha posidoniae* Picard, 1951: 341, fig. 2B.

Description

Details of structure conforming well with previous descriptions. Thickness of perisarc variable, young hydrocladia with no internodal septa behind hydrotheca, old ones with two strong septa.

Hydrotheca with an abcauline wall which is gently curved throughout or straight in the distal half.

Lateral nematothecae with the upper (abcauline) surface strongly cut away, as described by Bale.

Measurements (mm)

Stem, internode length	0,26–0,44
Hydrocladium, thecate internode, length	0,17–0,23
Hydrotheca, abcauline height	0,17–0,21
diameter at margin	0,14–0,16

Remarks

Picard (1951) has described a new species from the Mediterranean, *P. posidoniae*, which is said to differ from *P. obliqua* in the deeper hydrotheca, more convex abcauline wall and better developed perisarc. He includes Bale's

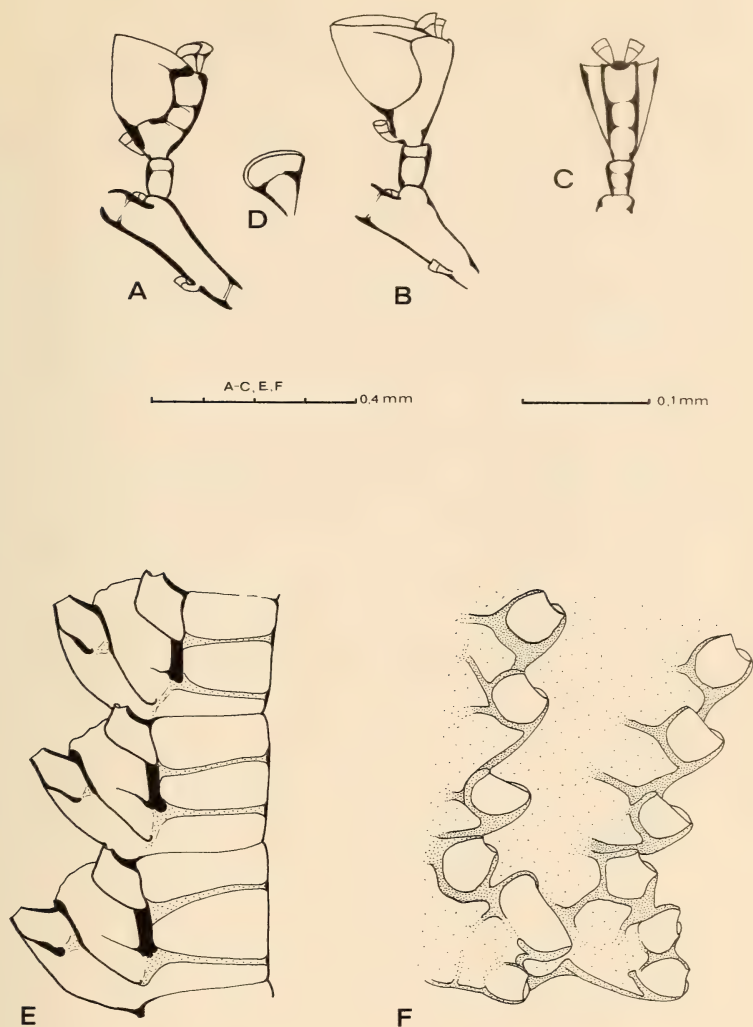


Fig. 8.

A-D. *Plumularia obliqua*. A and B, hydrocladia in side view, A with well-marked internodal septa, B without; C, hydrocladium in posterior view; D, lateral nematotheca. All from the same colony. E-F. *Aglaophenia cupressina*. E, part of a hydrocladium; F, the proximal part of two corbula ribs from the side.

material from Australia in this species. The present material shows sufficient variation to cover both and it is felt that there is little justification for a separate species. Picard gives no measurements and does not describe the structure of the lateral nematothecae.

This is the first record of the species from the East African coast.

Aglaophenia cupressina Lamouroux, 1816

Fig. 8 E, F

Aglaophenia cupressina Lamouroux, 1816: 169. Billard, 1913: 107, fig. 96; pl. 6. Bale, 1915: 319; pl. 47, figs 6-8.

Aglaophenia macgillivrayi: Allman, 1883: 34; pl. 10; pl. 20, figs 4-6.

Description

Several robust colonies of this beautiful species. Main stem branching and rebranching irregularly up to the fourth order. Final branches (pinnae) arising at regular intervals in subopposite pairs, bearing alternate hydrocladia. Hydrocladia also present on more distal parts of stem and larger branches.

Details of hydrocladia, hydrothecae and nematothecae as in previous descriptions. The slight longitudinal ridge down the centre of the lateral surface of the hydrotheca mentioned by Bale visible in macerated specimens only. Hydrotheca 0,25-0,28 mm in depth and 0,14-0,15 mm in marginal diameter. Margin smooth or sinuated, often with two or three pairs of low rounded lobes.

Corbulae abundant, replacing hydrocladia, with a pedicel of one thecate segment and about six pairs of ribs, completely closed, reaching 2,8 mm in length and 1,1 mm in diameter. The first two or three nematothecae of the rib seated on a raised lobe. Some corbulae with a free branch to the first rib of one side.

Remarks

This well-known Indo-Pacific species has been reported from Zanzibar on the East African coast by Kirchenpauer (1872, as *A. spicata*) and by Jarvis (1922). This is the most southerly record for the African coast.

Gymnangium gracilicaule lignosum (Millard, 1968)

Halicornaria gracilicaulis lignosa Millard, 1968: 283.

Remarks

These stems are not so woody or thick as is typical of this subspecies and most have only two orders of branching, one alone having three orders. They are probably young colonies.

The hydrotheca, however, is of the typical shape, i.e. short (about 0,23 mm in total height), with a pronounced sigmoidal curvature to the abcauline wall and a short distance (about 0,07 mm) between the abcauline margin and the point of separation of the median inferior nematotheca from the hydrotheca. The median inferior nematotheca is short and does not reach the level of the thecal margin.

Family **Proboscidae***Proboscidae* (Lar) sp.

Fig. 9

Description

Colonies growing on tubes of the polychaet, *Laonome* sp. Hydrorhiza reticular, spreading between the sand-grains of the polychaet tube. Gastrozooids forming a single row on rim of tube, reaching a maximum height (preserved) of 0,48 mm to tip of hypostome. Two solid filiform tentacles arising at half to two-thirds of height and facing cavity of polychaet tube. Hypostome with an asymmetrically placed pad of nematocysts on the side away from the cavity.

Gonozooids of varying size, the largest ones reaching 0,31 mm in height and seated immediately below the gastrozooids or arising from their bases, only these large gonozooids bearing medusa-buds. Smaller, sterile gonozooids scattered for some 2 mm down the length of the polychaet tube. Gonozooids without tentacles, with a distal pad of nematocysts, bearing up to four medusae of different ages.

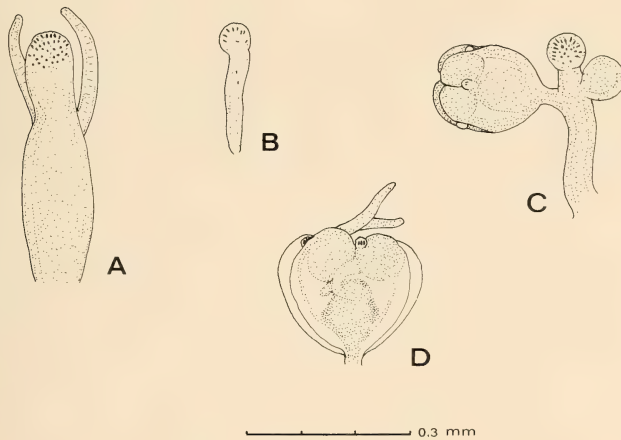


Fig. 9. *Proboscidae* (Lar) sp.

A. Gastrozooid. B. Sterile gonozooid. C. Fertile gonozooid with medusa-buds. D. An older medusa-bud.

Medusa with four perradial marginal bulbs each bearing a hollow tentacle, four interradial nematocyst sacs (cnidothylacies), four unbranched radial canals, stomach with the beginnings of four pouches, no ocelli. Largest medusa 0,23 mm in depth and 0,26 mm in diameter.

Nematocysts of three types:

- (i) Macrobasic euryteles, $13,2-15,6 \times 6,0-6,6 \mu$. Butt coiled in four whorls in the transverse axis. Discharged capsules similar to those illustrated

by Russell, 1938, for *Lar sabellarum*. Present in the nematocyst pads of the hydranths and in the cnidothylacies of the medusae.

- (ii) Microbasic euryteles, $5,4-7,8 \times 2,1-3,0 \mu$. None seen discharged.
- (iii) Desmonemes, $3,6-4,2 \times 2,4-3,0 \mu$.

Remarks

Identification of species of *Proboscidactyla* essentially depends on details of medusa structure, and as far as the hydranths go 'there appears to be no precise way to separate the various species' (Calder 1970). Hand (1954) advocates the use of small differences in nematocysts for this purpose, but this is of little help in the present material, for although the three categories characteristic of the genus are present, all are smaller than those described for any other species.

The hydranths of five species of *Proboscidactyla* are known, namely *P. circumsabella* Hand, 1954, *P. flavicirrata* Brandt, 1835, *P. occidentalis* (Fewkes, 1889), *P. ornata* (McCrary, 1857) and *P. stellata* (Forbes, 1846) = *Lar sabellarum* (Gosse, 1857). Of these, only *P. ornata* has been reported from the western Indian Ocean (Kramp 1965: near Mombasa). The life-history of this species has been described by Brinckmann & Vannucci (1965) and by Calder (1970). There is nothing to debar the present material from inclusion therein apart from nematocyst size, and nematocyst size must be variable for there are differences between the measurements given for this species by Brinckmann & Vannucci from the Mediterranean and those given by Calder from Virginia. However, it would be unwise to make a definite diagnosis until such time as the medusa has been reared.

SUMMARY

A collection of hydroids from the Inhaca area and from Santa Carolina on the Moçambique coast, East Africa, is described. The collection includes 86 species, of which one is new to science, namely *Hydrodendron sympodiformis*, and 19 are new records for Africa south of 20° S. Lat.

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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

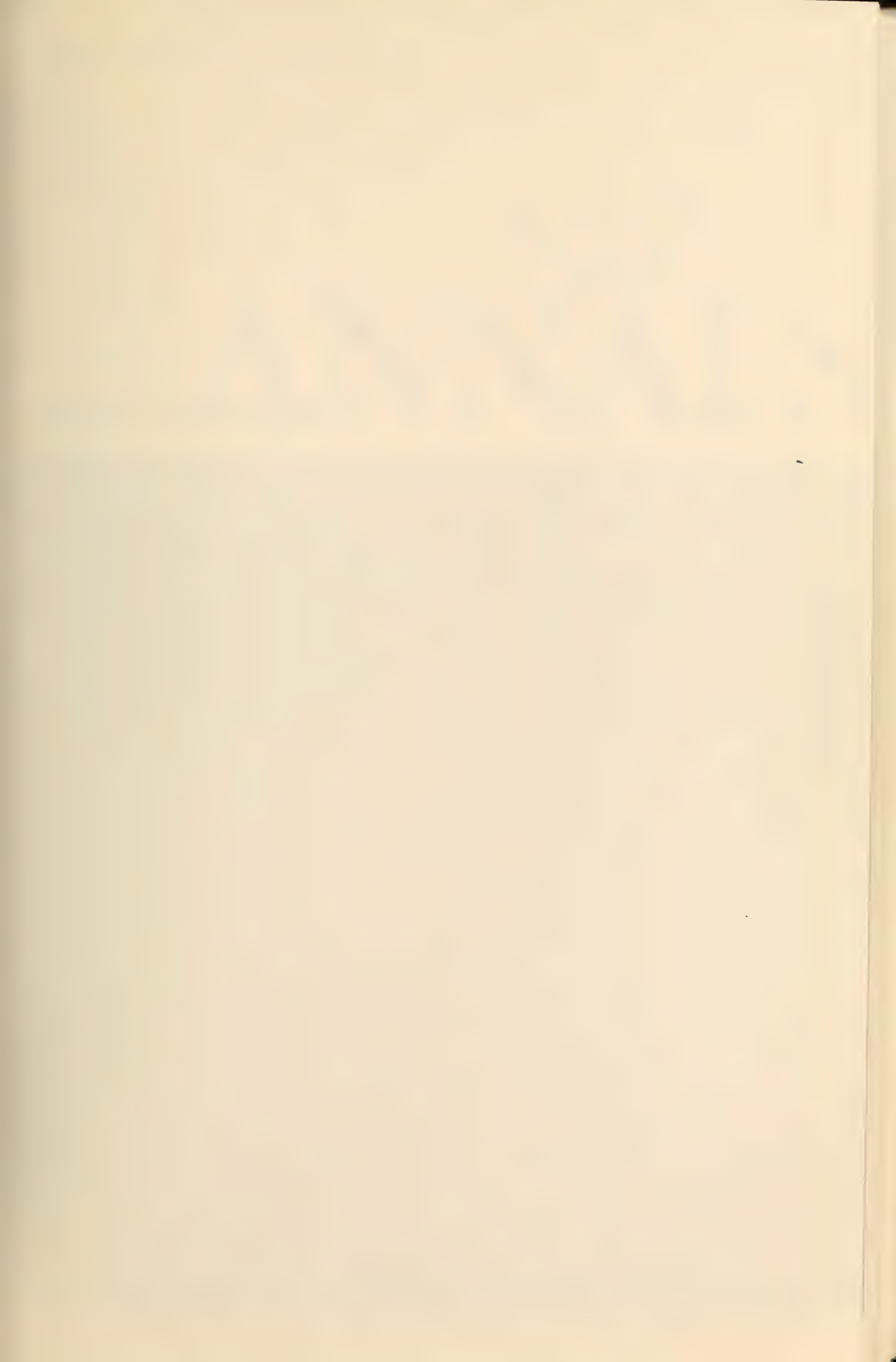
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N. A. H. Millard & J. Bouillon

A COLLECTION OF HYDROIDS
FROM MOÇAMBIQUE, EAST AFRICA

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MAY 1974

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THE EXTINCT CAPE COLONY QUAGGA,
EQUUS QUAGGA QUAGGA (GMELIN)

By
R. E. RAU

Cape Town Kaapstad

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R. E. RAU

South African Museum, Cape Town

(With 25 figures)

[MS accepted 12 June 1973]

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INTRODUCTION

Much has been written about the reason for the extinction of the quagga, *Equus quagga quagga* (Gmelin 1788). It is usually attributed to 'ruthless' hunting and even 'planned extermination' by the colonists of the bigger herbivorous animals, as these were considered to be competing against their livestock for grazing. The quagga, which existed in large numbers, is also said to have been hunted for its flesh, which the farmers fed to their labourers, and its skin, which was used for grainbags and leather. Because of the great demand in the hide trade for skins of quagga, zebra and other game, the farmers of the Orange Free State in the eighteen-sixties organized hunting expeditions to collect them. Wagon-loads of prepared skins were driven to the coast for sale (Bryden 1889: 401).

Eloff (1966) sees the reason for the extinction of the quagga in 'an ever greater pauperised gene pool relative to further migration southward, with decreasing adaptability to changed environmental conditions'.

The quagga had a comparatively small range, which is a known factor in the elimination of endemics. In addition, its range was restricted by farm fences (Jackson 1920), which separated groups and individuals from one another.

While the above factors may all have contributed to the disappearance of the quagga, there are another two which have not been mentioned by previous authors.

South Africa was for a long time known as a 'hunting paradise'. Many books, e.g. *Portraits of the game and wild animals of southern Africa* (Harris 1840), give evidence of the senseless mass killing by those privileged to journey to the Cape of Good Hope to satisfy their hunting urges. The quagga obviously experienced this onslaught.

The second factor was the years of drought, experienced after 1876, which could have been the final *coup de grâce* for the species. In his *Manna in the desert*, Alfred de Jager Jackson (1920) recalls his younger days on a Great Karroo farm near Nelspoort (the area from which the Cape Town quagga foal originated). He writes (p. 73): 'The last years of my life on the Karroo farm were clouded and sad. I would not care to live them again. As I have said, the good seasons ended in 1876. The year following was a time of dread disease and drought. The carcasses of thousands of dead animals lay rotting over the land.'

It has however also been stated that the species vanished without this fact having been noticed by zoologists. In Afrikaans the word 'Kwagga' was, and still is, used for the true quagga and for both plains zebra and the mountain zebra. Outside the Cape Colony 'Quagga', in its various spellings, implied *Equus quagga quagga* only. The first indigenous equids which the white settlers in South Africa became acquainted with were the true quagga and the mountain zebra. They referred to these as 'Kwagga', 'Wilde-esel' or 'Wildeperd', 'Gestreepte-esel' or 'sebra' (Scholtz 1941). With their advance in a northerly direction, the colonists met with Burchell's zebra, which they called the 'Bontkwagga'. Unfortunately in common usage in South Africa the 'Bont' is often dropped and 'Kwagga' was and still is 'good enough' to describe any striped equid.

It appears to be largely this confusion which led to the accidental disappearance of the quagga. Had the true situation been realized, when the quagga became rare in the middle of last century, efforts might have been made to protect the species in its native country and to breed from those in European zoos. (It should be noted that as early as 1822, when the need to protect the bontebok, *Damaliscus dorcas dorcas* (Pallas), was realized, this antelope was excluded from otherwise unspecified hunting licences, issued by the Colonial Office in Cape Town.)

Although it cannot be determined when the last indigenous quaggas disappeared, it is generally accepted that the female specimen which died at Amsterdam Zoo on 12 August 1883 outlived those in South Africa. A letter dated 6 November 1856 from A. Dale, Beaufort West District, to the director of the South African Museum states that 'Quaggas seem to be rather scarce', yet Mr Bols, the Belgian Consul at Port Elizabeth, still obtained 'several' quaggas in 1870; these were sent to Antwerp Zoo.

Several authors have discussed the striping and coloration of the quagga. Old descriptions and illustrations which were made from living specimens refer to animals with black or dark stripes on a brown or fawn base, while the legs and ventral surface are given as white or whitish. Later authors declare that these early descriptions were incorrect, due to carelessness, incompetence and inaccurate observation, and describe the quagga as dark brown, chestnut or fawn coloured with white or whitish stripes, restricted to the antero-dorsal region of the animal, while other zebra forms are described as being light with black-brown stripes. If the quagga is indeed a light-striped animal, how can the

presence of dark stripes or stripe fragments, posterior to the 'light-striped' portion and above the hooves, be explained?

With this in mind all quagga skin material in Europe, except for the foetus in Stockholm, the 'Elgin head' together with a mounted skin in Edinburgh and the material possibly existing in Russia, was examined by the author in 1971.

In common practice, the part which covers the smaller percentage of a bi-coloured surface is called the 'pattern'. The quagga has retained light interspaces on the anterior portion of the body. These interspaces are, in contrast to other members of the plains (or Burchell's) zebra group, only half, or less than half, as wide as the stripes. As these light regions cover a lesser proportion of the animal than the dark, it has in publications of this century been described as a light-striped animal.

As an adaptation to open country, the plains zebra group, including the quagga, exhibits progressive reduction in striping and contrast between stripes and interspaces from the north to the south of its range, i.e. the white darkens towards brown, the black lightens to a brown. This process, which commences from the hooves and from the buttocks, culminates in the disappearance of stripes.

The quagga represents the extreme limit of this trend. The unstriped postero-dorsal region of the animal is of a brown tone, which is intermediate between the light and dark colours of the clearly striped antero-dorsal region.

The difference in coloration between northern and southern sub-species of plains zebra appears to have been achieved by changing the pigment distribution. It seems therefore that in the quagga the proportion of light and dark pigments is the same as in other members of the plains zebra group.

Examination of single hairs from various portions of the quagga reveals that the areas between striped and unstriped regions are occupied by multi-coloured hairs. Each hair shows light and dark transverse sections, similar to the colour pattern of individual porcupine quills. Hairs from faint stripes have a higher proportion of dark sections than hairs from the interspaces. The interspaces, which show progressive darkening towards the posterior region of the animal, may be distinguished, even in the regions with faint stripes or stripe fragments, by their lighter colour. Hairs from other parts of the body are uniform in colour and are light, dark or of intermediate tone, according to their position. This type of pigmentation is particularly obvious in the Berlin, Vienna and Amsterdam specimens.

Parallel with this reduction of contrast and striping is the occurrence and progressive intensification of shadow-stripes (darkish streaks within the interspaces). In southern forms of the plains zebra this has reached the stage where, on the buttocks, it has become difficult to distinguish stripes from shadow-stripes.

In the quagga this has been carried further. The region anterior to the unstriped area is covered with numerous narrow, dark stripes or stripe fragments, about twice the number as in the similar region of a plains zebra. Some

of these narrow bands are obviously stripes while others are shadow-stripes. This can be seen clearly in the Basle and Paris specimens.

The next stage in this process appears to be the fusion of shadow-stripes with the true stripes, which produces the wide stripes characteristic of the quagga. Often fragments of interspaces are retained, forming light dots or streaks within the stripes. In regions where there is little fusion between fragments of stripes and shadow-stripes, a dappling effect is often produced. This has presumably led to illustrations like the one by Ridinger.

Whether the quagga represents a species or subspecies, and whether differentiation by colour characteristics can be applied, have been much discussed. Hilzheimer (1912) considered that the narrow interspaces (hell gestreift) were diagnostic. He therefore accepted the Wiesbaden specimen as a true quagga, although he could not fit this specimen into the stripe-reduction sequence suggested by Ridgeway (1909).

At first sight, the narrow interspaces and very reduced body striping appear to be characteristic of the quagga, as is the reduced striping on the face (between eye and corner of mouth) and broad dorsal median stripe, together with its indicated or continuous flanking band on each side. However, all these characters are variable and are independent of one another. On the basis of only one of these four colour characteristics there is no sharp division between *Equus q. burchelli* and *Equus q. quagga*. The preserved quagga specimens continue the gradual change in colour and in marking shown by the north to south colour variants of the plains zebra group. The advanced example would have no facial striping, body stripes terminating at the shoulder, interspaces one-third or less the width of the stripes, and a broad dorsal median stripe with a continuous flanking band on each side.

Because of missing markings below the fork of the shoulder-stripe and below the last body stripe, Hilzheimer (1912) erected the subspecies '*paucistriatus*' of *Equus burchelli*, for two of the four Mainz specimens. (He considered that the 'lack' of the ventral median stripe in the type might be characteristic, but traces of this stripe can still be seen in the specimen. The Darmstadt and Munich specimens also show this and there is no doubt that the 'absence' of the ventral median stripe must be attributed to taxidermy. Furthermore the second specimen of '*Equus burchelli paucistriatus*' in Mainz possesses a ventral median stripe.)

If *Equus quagga quagga* can be identified by the presence of at least two of the four characteristics, then the long-haired female '*Equus burchelli paucistriatus*' at Mainz is a true quagga, since it possesses narrow interspaces, faintly striped face and broad dorsal median stripe, flanked with almost continuous bands. Similarly the specimens at Tring and Vienna must be identified as *Equus quagga quagga*. The former has a faintly striped face and broad dorsal median stripe, flanked with interrupted light bands. The latter, in spite of marking below the shoulder-stripe fork and last body stripe has narrow interspaces and a broad dorsal median stripe, flanked with interrupted light bands. These

specimens represent the variation of the quagga closest to *Equus q. burchelli*, while the type of '*Equus burchelli paucistriatus*' represents the variation of *Equus q. burchelli* closest to *Equus q. quagga*. Thus the museum at Mainz has three true quaggas, as suggested by Schwarz (1912), and also, of the preserved specimens of *Equus q. burchelli*, the closest to the true quagga.

To summarize, the colour and markings of the preserved quagga specimens do not support the identification of the quagga as a separate species, as suggested by the following authors, some of whom have studied skulls and skeletons as well: Hilzheimer (1912), Cabrera (1936), Allen (1939, 1945), Cooke (1943), Lundholm (1951), Roberts (1951), Ellerman *et al.* (1953), Meester (1964), Ansell (1967).

The question has been raised as to whether or not the colour and pattern variation within the preserved quagga skins represents geographical forms. As only a few skins have precise locality data, this has remained unanswered. However, Antonius (1931) concluded that quaggas with both few and many stripes might have occurred throughout the distribution area. This seems to be confirmed by the following extract from a letter dated 11 June 1857 (1858) to the director of the South African Museum from A. Dale of Kampherskraal at 'Nell's Poort' (Beaufort West District) announcing the arrival of the Cape Town foal: 'I believe there are two kinds, the stripes of the one kind being more indistinct and of much paler colour than those of the other: this is a specimen of the dark striped kind; the one which the Governor possesses and which was reared at Nell's Poort is of the other description.' (Dale's differentiation might be due to the much darker appearance of a less striped animal compared with a more extensively striped individual.) The colour variation within the preserved skins, where not due to fading or individual variation, could however also be the result of seasonal changes.

An interesting point arises in connection with the Governor Sir George Grey's specimen. On 4 September 1858 he donated a quagga to London Zoo, Regent's Park. This male, of which a high-quality drawing by H. Weir appeared in *Illustrated London News*, volume 33, 6 November 1858, had to be killed because of self-inflicted injury on 10 June 1864. The mounted skin and skeleton at the British Museum (Natural History), London, which were entered in the catalogue on 2 July 1864, were regarded as those of Grey's animal. However, I have examined the skin and have found it to be that of a female, while the skeleton is that of a male, if the presence of large canines can be accepted as a means of identification. The shattered left metacarpal, as Dr A. W. Gentry of the British Museum pointed out to me, seems to indicate that the skeleton at least is of Grey's animal. It is feasible that when Grey's animal became available in 1864 the British Museum decided to buy a more characteristic and already stuffed skin from the Zoological Society's Museum, which was most likely that of the first London Zoo specimen which had died in 1834 (Shortridge 1934) and to obtain or keep only the skeleton of Grey's animal.

In trying to identify the illustration of Grey's animal with one of the stuffed

skins of which no data are available, the following became evident. Grey's animal was peculiar in having fragments of transverse stripes on the rump, resembling the gridiron pattern of *Equus zebra*. This atypical marking is found only in the Wiesbaden specimen, a male, and it is considered that this specimen is the skin of Grey's animal. Furthermore, the Wiesbaden specimen apparently does not contain a skull or footbones (a practice unusual in taxidermy at that time), and the skin is repaired in the area of the left metacarpal, the region of the self-inflicted injury. The Wiesbaden specimen was bought from the dealer Frank of Amsterdam in 1865. It is known that Frank dealt in quagga material with the dealer Edw. Gerrard of London (Tring specimen), but no records of transactions regarding Grey's dead animal, nor of its disposition by the London Zoo, could be traced.

Although the Governor did have a private menagerie at Cape Town (Anon 1858), there are no records of any other quaggas in it. If the above assumption is correct and the Governor's quagga referred to by Dale was the male donated to London Zoo, i.e. the Wiesbaden specimen, then there is confirmation that the two extreme forms of quagga, as exemplified by the Cape Town and Wiesbaden specimens, occurred in the same locality.

Mention should also be made of the second London Zoo quagga (1851-72), a female, which is the only quagga ever photographed alive in Europe. According to previous authors the skin of this animal was not preserved, as it was bad (Ridgeway 1909). However, comparison of the photographs with the stuffed specimen in the Royal Scottish Museum, Edinburgh, reveals that the two are one and the same specimen. It appears, therefore, that the skin was not discarded, but was sold to the Museum in 1879 by Edw. Gerrard. The skeleton of this specimen has recently been discovered in the collection of the Peabody Museum of Natural History, Yale University (Willoughby 1966).

The locality given for the Leiden quagga—Steenbergen, Cape Colony—is incorrect. The position of the only 'Steenbergen' ever recorded is in the Cape Peninsula, well outside the known distributional range of the quagga. This mistake apparently stems from one of the two labels included with this specimen. The two labels give different data: (i) 'obtained alive in 1826'; (ii) '15th June, 1827—Steenbergen'. As can be seen below, neither of the labels is likely to apply to this specimen. It is possible that (i) refers to the female specimen discussed below, while (ii) probably refers to a male mountain zebra specimen (*Equus zebra*) sent to Leiden in conjunction with a quagga. This mountain zebra could well have been collected at Steenbergen.

During the years 1827-33, the Cape Town based medical doctor and agent for the Rijksmuseum van Natuurlijke Historie in Leiden, H. B. van Horstok, sent three quagga specimens to Leiden. The first, a female, he obtained alive, but unfortunately the animal died before shipment, so that only its skin and skeleton were sent to Leiden, as announced in Van Horstok's letter to the director, dated 1 July 1827. The second specimen, a male, together with a male mountain zebra, was shipped on the frigate *Bellona* and was received by the

director of the navy in Holland in July 1830. The third specimen, of indeterminate sex, which Van Horstok obtained from 'Graaf Reinjet' on 25 March 1831 was dispatched to Leiden on or about 20 May 1833, the date of the letter which announced the dispatch.

As far as is known, the Rijksmuseum van Natuurlijke Historie handled only these three quaggas of which there are today only one mounted stallion and a skeleton at Leiden. However, the immature quagga skeleton at Berlin is said to have been exchanged with the Rijksmuseum van Natuurlijke Historie in 1833-8 (Opperman 1970).

The policy at the Rijksmuseum van Natuurlijke Historie at that time was to keep a perfect male, female and juvenile specimen of every species and to exchange or sell any additional or imperfect specimens. (Van Bruggen, personal communication.)

On 3 August 1830 a quagga (skin and male skull) was dispatched from Leiden to the Senckenberg Museum in Frankfurt, where it was received in 1831.

Renshaw (1904) suggested the possibility that the Turin specimen may have been collected by Van Horstok. This female specimen, which was bought in 1827 by the Turin museum from the dealer S. Leadbeater of London, is damaged and has a sewn cut on the right side of the dorsal median stripe. These facts, when considered in the light of the policy of the Rijksmuseum van Natuurlijke Historie, appear to suggest that the Turin specimen might be the first (female) Leiden quagga. It is however difficult to imagine that the specimen which arrived in Holland probably late in 1827 could have been mounted, sold to Leadbeater and from there to Turin, all within that year.

Unfortunately no certainty about the Leiden quaggas could be reached.

The history of the Tring specimen must be mentioned. On 2 April 1842 Lord Derby requested a live male quagga from his Cape Town agent, the Reverend John Fry (xerox copy of letter at the South African Museum, Cape Town). Lord Derby had at his Knowsley menagerie a female quagga, which might have been obtained from Fry. After Derby's death his animals were sold in 1851. It appears that the male quagga had died previously. The female was sold to Amsterdam Zoo, and was stuffed when it died there in 1853. After the last living quagga had died in 1883 and been mounted, the Amsterdam Museum may have sold its earlier specimen to the dealer Frank of Amsterdam, who is known to have bought a mounted quagga as a 'duplicate from a continental museum' (Renshaw 1904). Frank sold this specimen to Edw. Gerrard of London, who re-mounted it and sold it in 1889 to Lord Rothschild of Tring. That the Tring specimen might in fact be the Knowsley female seems proven by the specimen's old label 'From E. Gerrard, Jun., 61 College Place, Camden Town, London—Quagga *Equus quagga* Linn. Gray Knowsley Menagerie—South Africa'. Supporting this is the resemblance between the Tring specimen and the animal on the right in Hawkins's drawing (Gray 1850) of the live Knowsley quaggas. It is obvious that the artist did not make a completely correct picture, nevertheless characteristics like the big light patch in one of the last of the

body stripes on the left and the dorsal forking of some body stripes are found in both.

Although there have been attempts to breed quagga in captivity there are apparently no records of this. However there are records of the birth of quagga hybrids (Wagner 1835; Renshaw 1904, 1935) with either a male or female quagga parent. In one instance, the female horse-quagga hybrid proved to be fertile and was crossed with an arab stallion, the resulting offspring resembling the quagga in its mane and body striping (Wagner 1835).

None of these hybrids is preserved, but according to descriptions they differed from hybrids of other zebra forms. These have clear, zebra-like leg striping while the quagga hybrids have few leg stripes, mainly at the 'knees' and 'hocks', and striping on the neck and shoulder. This leg striping in the hybrids, which should not be confused with faint markings just above the hooves, traceable in most preserved quagga skins, is interesting since the quagga parent in each case must have had plain coloured legs.

The stuffed equid foal in the Museum and Art Gallery at Doncaster, Yorkshire, which has not been previously recorded in the literature, exhibits the characteristics of quagga hybrids. It appears to be the only quagga hybrid skin still in existence. While the label on the outside of the original showcase reads: 'Zebra-foal born at Owston, 1st April 1830', there is an old label attached to the specimen, naming it as a 'cross between a male ass and a female quagga'. This foal in its case was donated to the museum by the Davies-Cooke family in 1923. Phillip Davies-Cooke brought a 'zebra' from the Cape in the early nineteenth century. This animal was in all probability the mother of the foal which is now in the Doncaster Museum. The skeleton which Davies-Cooke donated to the Yorkshire Philosophical Society in 1841 is most probably that of the mother.

Two further unusual equid hybrids, both with the same parents, are preserved in the Tring Museum. They were born in Lord Rothschild's menagerie at the end of the nineteenth century and are the result of a cross between a male horse and a female Burchell's zebra. Their striping is similar to that of the foal at Doncaster, but is more intensive and extends further posteriorly. The larger of the two shows quite strong but narrow dark stripes on the buttocks. It seems quite likely that their mother was in fact a specimen of *Equus quagga burchelli*.

LIST OF INSTITUTIONS HOUSING QUAGGA MATERIAL

Some inaccurate statements concerning the preserved quagga material are to be found in the literature, including the lists by Renshaw (1904), Ridgeway (1909), Hiltzheimer (1912), Harper (1945) and Rzasnicki (1949); these errors are corrected in the following list. The osteological material not belonging to skins is listed without guarantee of correct identification and is based only on information given by the institutions concerned or previous authors.

Place	Sex	Skin	Complete skeleton	Skull	Loose bones	Institution	Address
Amsterdam	♀	+	—	+	—	Zoölogisch Museum	Plantage Middenlaan 53 Amsterdam-C Netherlands
Bamberg	♀?	+	—	+	—	Naturkunde Museum	Fleischstrasse 2 D-86 Bamberg W. Germany
Basle	♀	+	—	+	+	Naturhistorisches Museum	Augustinergasse 2 CH-4051 Basle Switzerland
Berlin	♀	+	—	+	—	Museum für Naturkunde an der	Invalidenstrasse 43 X-104 Berlin
Bristol*	juv.	—	+	—	—	Humboldt Universität	Germany
	♂	—	—	+	—	City Museum, Department of Natural History	Queen's Road Bristol BS8 1RL England
Cape Town	♀ foal	+	—	+	+	South African Museum	Queen Victoria Street P.O. Box 61, Cape Town, South Africa
Darmstadt	♀	+	—	—	—	Hessisches Landesmuseum, Zoologische Abteilung	Friedensplatz 1 D-61 Darmstadt W. Germany
Edinburgh	? ♀	head +	— —	(+) —	— —	Royal Scottish Museum	Chambers Street Edinburgh EH1-1JT Scotland
Frankfurt	♂	+	—	+	—	Natur Museum Senckenberg	Senckenberg-Anlage 25 D-6 Frankfurt/Main 1 W. Germany
Kazan		+				Zoological Museum	University Kazan, USSR
Leiden	♂	+	+	—	—	Rijksmuseum van Natuurlijke Historie	Raamsteeg 2 Leiden, Netherlands
London	♀	+	—	—	—	British Museum	Cromwell Road
	♂	—	+	—	—	(Natural History)	London SW7 5BD England
London	♀	—	+	—	—	University College, Department of Zoology	Gower Street London WC1E 6BT England
Mainz	♂	+	—	—	—	Naturhistorisches Museum	Reichklarastrasse 1 D-65 Mainz W. Germany
Milan	♀	+	—	—	—	Museo Civico di Storia Naturale	Corso Venezia 55
	foal	+	—	(+)	—		I-20121 Milan Italy
Munich	♀ imm.	+	—	(+)	—		
	♀	+	—	+	—	Zoologische Sammlung des Bayerischen Staates	Schloss Nymphenburg Nordflügel D-8 Munich 19 W. Germany
	♂	—	—	+	—		
New Haven	♀	—	+	—	—	Peabody Museum of Natural History, Yale University	New Haven Conn. 06520, U.S.A.

* See footnote on page 57.

Place	Sex	Skin	Complete skeleton	Skull	Loose bones	Institution	Address
Paris	♂	+	+	—	—	Museum National d'Histoire Naturelle, Laboratoire de Mammalogie	55 rue de Buffon Paris—5e France
Philadelphia	♂	—	+	—	—	The Academy of Natural Sciences	Nineteenth and the Parkway Philadelphia Penn. 19103, U.S.A.
Pretoria	♀	—	—	+	—	Transvaal Museum	Paul Kruger Street PO Box 413 Pretoria, Transvaal South Africa
Stockholm	foetus	+	—	—	—	Naturhistoriska Riksmuseet	Roslagsvägen 124 S-104 05 Stockholm 50 Sweden
Stuttgart	♀	—	—	+	—	Staatliches Museum für Naturkunde	Schloss Rosenstein D-7 Stuttgart 1 W. Germany
Turin	♀	+	—	+	—	Museo e Istituto de Zoologia Sistemática	Via Gioletti 34 I—10123 Turin Italy
Tring	♀	+	—	—	—	Zoological Museum (affiliated to the British Museum (Natural History))	Akeman Street Tring, Herts. England
Tübingen	♂	—	—	+	—	Zoologisches Institut der Universität	D-74 Tübingen W. Germany
Vienna	♀	+	—	—	—	Naturhistorisches Museum	Burgring 7 A-1014 Vienna 1 Austria
Wiesbaden	♂	+	—	—	—	Städtisches Museum, Naturwissen- schaftliche Abteilung	Rheinstrasse 10 D-62 Wiesbaden W. Germany

+ = present;
 (+) = present in mount;

— = not present;
 ‡ = incisivae only.

LOST MATERIAL

Rzasnicki (1949) expressed the fear that a post-war inventory of quagga material might reveal many losses. The following specimens have indeed been lost, in some cases as a direct consequence of World War II.

AMSTERDAM: A female quagga skeleton was mounted for the Amsterdam museum; the whereabouts of the specimen are unknown (Tuijn 1966).

GRAHAMSTOWN: The quagga skull was destroyed by fire in 1942.

KOENIGSBERG: The mounted specimen was lost when 'Waldhof', a near-by castle used for safe storage by the museum, was burnt down at the end of the war.

LONDON: The two male skulls, housed in the Royal College of Surgeons, were destroyed during the bombing raids on that city.

MAINZ: The foal was partly destroyed by fire during World War II. Only the head, front legs and rump with hind legs and tail have been salvaged. Schwarz (1912) mentioned a male quagga skull as being in the collection of the Naturhistorisches Museum. This skull no longer exists nor are there any records of it.

MANCHESTER: Renshaw (1904) lists a quagga skeleton at the medical museum of the University. This specimen no longer exists, nor are there any records of its fate.

STUTT GART: Although Hilzheimer (1912) has described and figured quagga foot and leg bones housed in Stuttgart, these bones no longer exist nor is there any record of their disposition. The bones belonged either to the skin sent from Cape Town in 1827 by Von Ludwig to Tübingen or to the Amsterdam specimen.

YORK: A quagga skeleton was donated to the Yorkshire Philosophical Society (*Annual Report* 1841) by Ph. Davies-Cooke. The specimen no longer exists, nor are there any further records.

DESCRIPTION OF PRESERVED MATERIAL

EXPLANATION OF TERMS

Face: area between eye and corner of mouth

Interspace: light portion of colour pattern

Stripe: dark portion of colour pattern

Head-body: following contour of dorsal mid-line, except for portion between upper lip and posterior margin of nostrils and middle of rump to extreme posterior margin of buttocks, where the ruler remained straight. From anterior end of muzzle and posterior end of buttock a line to meet ruler in a 90° angle was imagined

Tail: from where it leaves body to flesh tip, leaving out the brush

Ear: along mid-line of outer surface, from head to tip

Hindfoot: along lateral side from 'sole' of hoof to middle of fetlock, from there to middle of heel

Shoulder height: vertically from base to highest point of withers

All measurements were taken by the author except for the specimens at Edinburgh, Doncaster and Stockholm.

Bones belonging to skins: not listed separately.

Bones belonging to skins but at different institutions: listed separately.

The references cited exclude the numerous illustrations, with or without short notes, when these contribute no specific information.

The type of *Equus burchelli paucistriatus* (Hilzheimer 1912) is included as the coloration of the specimen is intermediate between that of *Equus quagga burchelli* and *Equus quagga quagga*. It was considered synonymous with the true quagga by Allen (1939). The foal at Doncaster is included, as it appears to be the only quagga hybrid preserved.

AMSTERDAM—mounted skin and skull



FIG. 1. Amsterdam quagga.

Catalogue number: ZMA 522

Sex: female

Locality: —

Date of acquisition: 1883

Remarks on acquisition: animal lived at Amsterdam Zoo, 9 May 1867–12 August 1883

History of mount: original mount by Inspector Kerz (Hilzheimer 1912: 91)

Description of striking features: face fairly striped; light flanking bands of dorsal median stripe not interrupted; hair very short, transversely multicoloured in some regions; dark portions of animal umber, not the usual chestnut colour

Measurements: head-body: 2,28 m
tail: 0,46 m
ear: 0,16 m
hindfoot: 0,46 m
shoulder height: 1,20 m

State of preservation: very good

Further material of same individual: skull in collection. It appears from Hilzheimer (1912: 98) that the foot bones of this specimen were at Stuttgart but they are no longer there, nor is there any record of them

Remarks: not exhibited

References: Lydekker (1904); Renshaw (1904); Ridgeway (1909); Hilzheimer (1912); Griffini (1913); Antonius (1931); Van Bruggen (1959)

BAMBERG—mounted skin



FIG. 2. Bamberg quagga.

Catalogue number: 236 (mammal catalogue)

Sex: female?

Locality: —

Date of acquisition: 9 November 1858

Remarks on acquisition: bought as stuffed specimen from Dr F. Krauss, Stuttgart (Antonius 1931)

History of mount: re-mounted in 1969 by dermo-sculptor Kaestner, Berlin

Description of striking features: face unstriped; light flanking bands of dorsal median stripe not interrupted

Measurements: head-body: 1,935 m
tail: 0,410 m
ear: 0,165 m
hindfoot: 0,490 m
shoulder height 1,100 m

State of preservation: good

Further material of same individual: —

Remarks: exhibited open; alien matter used for improvement

References: Schwarz (1912); Antonius (1931)

BASLE—mounted skin, skull and foot bones



FIG. 3. Basle quagga.

Catalogue number: 897

Sex: female

Locality: received from Shiloh/Whittlesea, Eastern Cape Province

Date of acquisition: 1862/63

Remarks on acquisition: donated by missionary S. Gysin at Shiloh

History of mount: re-mounted in 1929 by dermo-sculptor G. Ruprecht

Description of striking features: face faintly striped near eye; light flanking bands of dorsal median stripe several times interrupted in anterior portion

Measurements: head-body: 2,14 m
tail: 0,38 m
ear: 0,15 m
hindfoot: 0,47 m
shoulder height: 1,20 m

State of preservation: good

Further material of same individual: skull (No 2860) and skeletal parts (No 8099, 10304) in collection

Remarks: exhibited

References: Ridgeway (1909); Roux (1910); Griffini (1913); Antonius (1931)

BERLIN—mounted skin and skull



FIG. 4. Berlin quagga.

Catalogue number: 4832 (old number: A1133)

Sex: female

Locality: —

Date of acquisition: 1867

Remarks on acquisition: animal lived at Berlin Zoo, 1863–7

History of mount: original mount (stuffed with straw)

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe not interrupted; animal very dark; hairs of faint striped regions with light and dark transverse sections

Measurements: head-body: 2,20 m
tail: 0,35 m
ear: 0,15 m
hindfoot: 0,47 m
shoulder height: 1,11 m

State of preservation: good, probably not faded

Further material of same individual: skull in collection

Remarks: not exhibited

References: Renshaw (1904); Ridgeway (1909); Hilzheimer (1912); Antonius (1931, 1951); Opperman (1970); Liversidge & ffolliott (1971)

BERLIN—skeleton

Catalogue number: 38954 (old number: An 8954)

Sex: immature

Locality: —

Date of acquisition: 1833–8

Remarks on acquisition: from anatomical collection J. Müller, exchanged with Rijksmuseum van Natuurlijke Historie, Leiden

Further material of same individual: —

References: Renshaw (1904); Ridgeway (1909); Hilzheimer (1912); Antonius (1931); Opperman (1970)

BERLIN—skull

Catalogue number: 23707 (old number An 1407)

Sex: male

Locality: —

Date of acquisition: 1833–8

Remarks on acquisition: from anatomical collection J. Müller

Further material of same individual: —

References: Renshaw (1904); Ridgeway (1909); Hilzheimer (1912); Antonius (1931, 1951); Opperman (1970)

BRISTOL—skull*

Catalogue number: Aa 3294

Sex: male

Locality: —

Date of acquisition: probably 1927

Remarks on acquisition: registered 1927

State of preservation: right PM₁ missing

Further material of same individual: —

CAPE TOWN—mounted skin, skull and footbones



FIG. 5. Cape Town quagga foal.

Catalogue number: SAM 35575

Sex: female, foal

Locality: Nelspoort, Beaufort West District, Cape Province

* In January 1974, while this paper was in press, Dr A. W. Gentry identified this skull as that of *Equus caballus*.

Date of acquisition: 1857–60

Remarks on acquisition: donated by A. Dale of Campherskraal, Nelspoort; animal lived one week after capture

History of mount: stuffed with hemp and clay at South African Museum; re-mounted by dermo-sculptor R. Rau 1969/70

Description of striking features: specimen with long, woolly fur (25–30 mm long); face faintly striped; light flanking bands of dorsal median stripe inconspicuous, not interrupted

Measurements: head-body: 1,240 m
tail: 0,280 m
ear: 0,123 m
hindfoot: 0,390 m
shoulder height: 0,770 m

State of preservation: good, partly moth-eaten

Further material of same individual: skull, footbones and fleshy parts of skin, all removed during re-mounting, in collection

Remarks: exhibited; since 1962 in special fade-ban glass case

References: Renshaw (1904, 1909); Ridgeway (1909); Antonius (1931); Shortridge (1934)

DARMSTADT—mounted skin



FIG. 6. Darmstadt quagga.

Catalogue number: HLM, M719

Sex: female

Locality: —

Date of acquisition: 1830

Remarks on acquisition: skin obtained from Stuttgart Museum (Scheer *in lit.* 1959); may possibly be the skin received in 1827 from Baron C. F. H. von Ludwig of Cape Town (Hilzheimer 1912)

History of mount: re-mounted in 1862 by Inspector Kerz (Hilzheimer 1912)

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe twice interrupted; ventral median stripe lost through taxidermy, except for anterior portion

Measurements: head-body: 2,260 m
tail: 0,520 m
ear: 0,165 m
hindfoot: 0,500 m
shoulder height: 1,200 m

State of preservation: good

Further material of same individual: it is likely that the skull at Stuttgart belongs to this animal

Remarks: exhibited

References: Hilzheimer (1912)

DONCASTER—mounted skin

(Hybrid *Equus q. quagga* ♀ & *Equus asinus* ♂)

FIG. 23

Catalogue number: 108.26

Sex: foal

Locality: born at Owsten, Yorkshire, 1 April 1830

Date of acquisition: 1923

Remarks on acquisition: foal died soon after birth; mounted by Hugh Reid, Doncaster, for Phillip Davies-Cooke, whose family donated it to the museum

History of mount: original mount

Description of striking features: faint striping traceable in most parts; several stronger stripes at withers and legs below 'knee' and 'hock', tail with long hair from the root, lower portion forming brush; mane and tail uniformly dark

Measurements: head-body: 1,170 m
tail: 0,280 m
ear: 0,105 m
hindfoot: 0,400 m
shoulder height: 0,780 m

State of preservation: good, probably faded

Further material of same individual: —

EDINBURGH—mounted skin



FIG. 7. Edinburgh quagga.

Catalogue number: 1879.35.1

Sex: female

Locality: —

Date of acquisition: 1879

Remarks on acquisition: bought from Edw. Gerrard, London; skin of London Zoo female, 15 March 1851 to 7 July 1872

History of mount: original mount

Description of striking features: face fairly striped; light flanking bands of dorsal median stripe not interrupted

Measurements: head-body: 2,205 m
tail: 0,400 m
ear, left: 0,150 m
ear, right: 0,145 m
hindfoot: 0,430 m
shoulder height: 1,170 m

State of preservation: good

Further material of same individual: skeleton at Peabody Museum of Natural History, Yale University, New Haven, U.S.A.

Remarks: Specimen is second Royal Scottish Museum quagga; first specimen (bought 1813, not 1818 as stated in the literature) no longer exists

References: Renshaw (1904); Ridgeway (1909); Antonius (1931)

EDINBURGH—mounted head

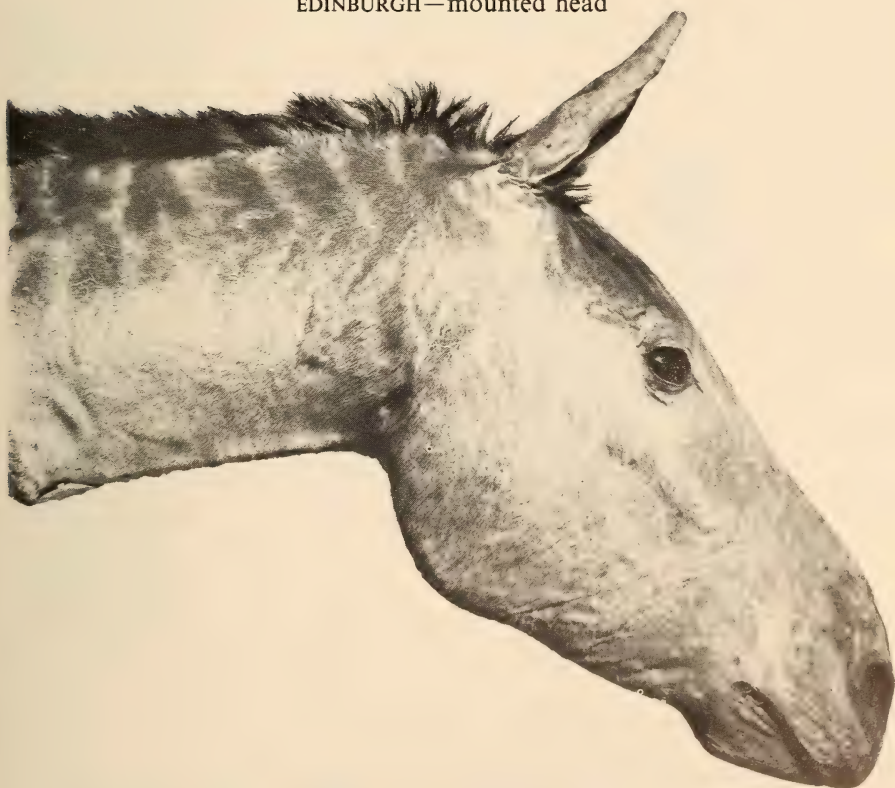


FIG. 8. Edinburgh quagga head (formerly Elgin).

Catalogue number: 1970-67

Sex: —

Locality: King William's Town, Cape Province

Date of acquisition: 1970

Remarks on acquisition: 1861 presented by John Maclean of King William's Town to Elgin and Morayshire Society, Elgin; 1970 sold to Royal Scottish Museum

History of mount: original mount, likely to have originated from complete mount

Description of striking features: face unstriped—probably through fading

Measurements: head, upper lip
to between ears: 0,415 m
ear, left: 0,170 m
ear, right: 0,150 m

State of preservation: much faded

Further material of same individual: skull is obviously inside mount

References: Ridgeway (1905, 1909)

FRANKFURT—mounted skin and skull



FIG. 9. Frankfurt quagga.

Catalogue number: 19207

Sex: registered as male, skin has no sexual organs

Locality: —

Date of acquisition: 1831

Remarks on acquisition: by exchange from Rijksmuseum van Natuurlijke Historie, Leiden; probably one of the three quaggas received by the Rijksmuseum between 1827 and 1833 from their agent at Cape Town, Dr H. B. van Horstok

History of mount: remounted at Frankfurt (Lotichius 1912)

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe, where preserved, only slightly interrupted

Measurements: head-body: 2,100 m
tail: 0,450 m
ear: 0,145 m
hindfoot: 0,450 m
shoulder height: 1,090 m

State of preservation: good, much patched

Further material of same individual: male skull in collection, occipital missing

Remarks: exhibited

References: Hilzheimer (1912); Lotichius (1912), Antonius (1931)

KAZAN—mounted skin

Catalogue number:

Sex:

Locality:

Date of acquisition: 1843

Remarks on acquisition: bought in Hamburg from a Mr Brandt by Professor Eversman for the Zoological Museum of Kazan University.

History of mount: it appears that this specimen was purchased as an old mount and remounted. In 1969 Mr Zaslavsky remounted specimen again

Description of striking features:

Measurements:

State of preservation:

Further material of same individual:

Remarks: the details given here were supplied to Dr V. Eisenmann, Paris, by Professor V. A. Popov, in charge of the Zoological Museum of Kazan University. No further information could be obtained directly from Kazan.

LEIDEN—mounted skin and complete skeleton



FIG. 10. Leiden quagga.

Catalogue number: 18243 (old number: Cat. Jentink 1892 No. a)

Sex: male

Locality: Cape Colony

Date of acquisition: 1830–3

Remarks on acquisition: specimen is probably the second or third of the three received by the Rijksmuseum van Natuurlijke Historie between 1827 and 1833 from their agent at Cape Town, Dr H. B. van Horstok

History of mount: original mount of straw. Specimen exhibited until 1913, causing slight fading of left side

Description of striking features: face clearly striped; mane hair very short; posterior neck stripes breaking up ventrally; light flanking bands of dorsal median stripe twice slightly interrupted anteriorly; posterior striping forming dappling; body stripes and dorsal median stripe with light streaks and dots; faint dark transverse bands above hooves

Measurements: head-body: 2,000 m
tail: 0,430 m
ear, left: 0,180 m
ear, right: 0,165 m
hindfoot: 0,470 m
shoulder height: 1,100 m

State of preservation: very good

Further material of same individual: complete skeleton in collection

Remarks: not exhibited; housed in total darkness

References: Renshaw (1904); Ridgeway (1909); Antonius (1931); Van Bruggen (1959)

LONDON, BRITISH MUSEUM (NATURAL HISTORY)—mounted skin



FIG. 11. London quagga.

Catalogue number: 1864.7.2.3. (old number: 1449a)

Sex: female

Locality: —

Date of acquisition: 1864

Remarks on acquisition: it seems probable that this specimen is the first London Zoo quagga, 5 November 1831–4 (Shortridge 1934; Antonius 1931; Sclater 1901). In 1864 the British Museum bought a stuffed quagga from

the museum of the Zoological Society and in the same year received at least the skeleton of the third London Zoo quagga, 4 September 1858–10 June 1864 (Sclater 1901; Renshaw 1904)

History of mount: original mount of straw

Description of striking features: face faintly striped; light flanking bands of dorsal median stripe twice interrupted on left

Measurements: head-body: 2,400 m
tail: 0,410 m
ear: 0,165 m
hindfoot, left: 0,480 m
hindfoot, right: 0,440 m
shoulder height: 1,180 m

State of preservation: poor, left ear off but present; skin cracked; crude repairs

Further material of same individual: the complete skeleton in the collection, which was believed to belong to this skin, is that of a male and probably that of the third London Zoo quagga whose skin is considered to be the one at Wiesbaden Museum

Remarks: not exhibited

References: Lydekker (1904); Renshaw (1904); Ridgeway (1909); Flower (1929); Antonius (1931)

LONDON, BRITISH MUSEUM (NATURAL HISTORY)—skeleton

Catalogue number: 1864.7.2.3. (old number: 1449a)

Sex: male

Locality: probably 'Nell's Poort', Cape Province

Date of acquisition: 2 July 1864

Remarks on acquisition: live animal received at London Zoo 4 September 1858

State of preservation: left metacarpal shattered

Remarks: it is considered that this skeleton belongs to the mounted skin at Wiesbaden, Germany

References: Sclater (1901); Lydekker (1904); Renshaw (1904); Ridgeway (1909)

LONDON, UNIVERSITY COLLEGE—skeleton

Catalogue number:

Sex: female

Locality:

Date of acquisition:

Remarks on acquisition:

State of preservation: left hind limb and right scapula missing

Remarks: Dr A. W. Gentry, British Museum (Natural History), is of the opinion that the specimen is *Equus quagga quagga*

MAINZ—mounted skin

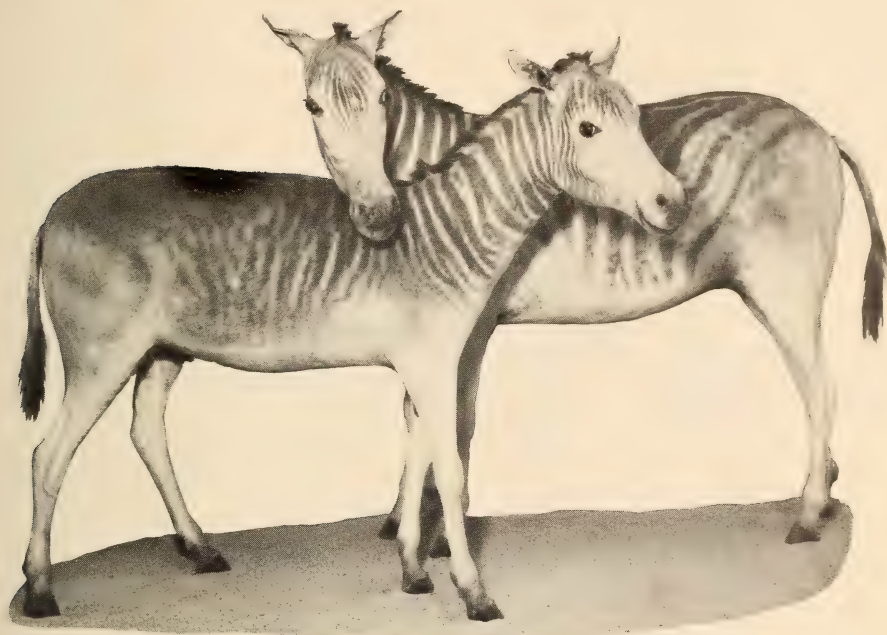


FIG. 12. Mainz, male quagga on left, Burchell's zebra (type of *Equus quagga paucistriatus* Hilzheimer, 1912) on right.

Catalogue number: 1955/13

Sex: male

Locality: —

Date of acquisition: 1840–50 (Hilzheimer 1912)

Remarks on acquisition: bought from dealer Rühl, Wiesbaden

History of mount: original mount

Description of striking features: face unstriped; light flanking bands of dorsal median stripe several times interrupted; shadow stripes on neck

Measurements: head-body: 2,020 m
 tail: 0,365 m
 ear: 0,150 m
 hindfoot: 0,440 m
 shoulder height: 1,130 m

State of preservation: fair, skin cracked

Further material of same individual: —

Remarks: exhibited

References: Hilzheimer (1912); Schwarz (1912); Antonius (1931)

MAINZ—mounted skin



FIG. 13. Mainz, female quagga.

Catalogue number: 1955/11

Sex: female

Locality: —

Date of acquisition: 1840–50 (Hilzheimer 1912)

Remarks on acquisition: bought from dealer Rühl, Wiesbaden

History of mount: original mount

Description of striking features: hair long, woolly; face faintly striped; light flanking bands of dorsal median stripe not interrupted, except for narrow contact with 1st pair of body stripes

Measurements:

head-body:	2,220 m
tail:	0,430 m
ear:	0,135 m
hindfoot:	0,430 m
shoulder height:	1,160 m

State of preservation: fair; skin cracked

Further material of same individual: —

Remarks: exhibited

References: Hilzheimer (1912); Schwarz (1912); Antonius (1931)

MAINZ—mounted skin



FIG. 14. Mainz, rescued portions of burnt foal.

Catalogue number: 1955/14

Sex: foal

Locality: —

Date of acquisition: 1840–50 (Hilzheimer 1912)

Remarks on acquisition: bought from dealer Rühl, Wiesbaden

History of mount: original mount

Description of striking features: face faintly striped; hair short

Measurements: head from upper lip

to between ears, straight: 0,245 m

tail: 0,190 m

hindfoot: 0,285 m

height at rump: 0,630 m

State of preservation: fair, partly destroyed by fire

Further material of same individual: skull inside mount (occipital burnt)

Remarks: not exhibited

References: Hilzheimer (1912); Schwarz (1912); Antonius (1931)

MAINZ—mounted skin

(Type of *Equus burchelli paucistriatus*)

FIG. 12

Catalogue number: 1955/12

Sex: female

Locality: —

Date of acquisition: 1840–50 (Hilzheimer 1912)

Remarks on acquisition: bought from dealer Rühl, Wiesbaden

History of mount: original mount

Description of striking features: face clearly striped; interspaces wide with shadow stripes; light flanking bands of dorsal median stripe present from lumbar region only; no markings below shoulder stripe fork and last body stripe

Measurements: head–body: 2,300 m

tail: 0,420 m

ear: 0,165 m

hindfoot: 0,460 m

shoulder height: 1,320 m

State of preservation: fair, skin cracked

Further material of same individual: —

Remarks: exhibited

References: Hilzheimer (1912); Schwarz (1912); Antonius (1931)

MILAN—mounted skin



FIG. 15. Milan quagga.

Catalogue number: not registered

Sex: female, immature

Locality: —

Date of acquisition: before 1848 (Sordelli 1909)

Remarks on acquisition: —

History of mount: original mount

Description of striking features: face unstriped; light flanking bands of dorsal median stripe several times interrupted; coat long and woolly

Measurements: head-body: 1,820 m
tail: 0,370 m
ear: 0,175 m
hindfoot, left: 0,460 m
hindfoot, right: 0,435 m
shoulder height: 1,020 m

State of preservation: fair, much faded, partly moth-eaten

Further material of same individual: skull or part thereof inside mount, upper and lower incisors visible

Remarks: exhibited

References: Sordelli (1909); Griffini (1913)

MUNICH—mounted skin and incisivae

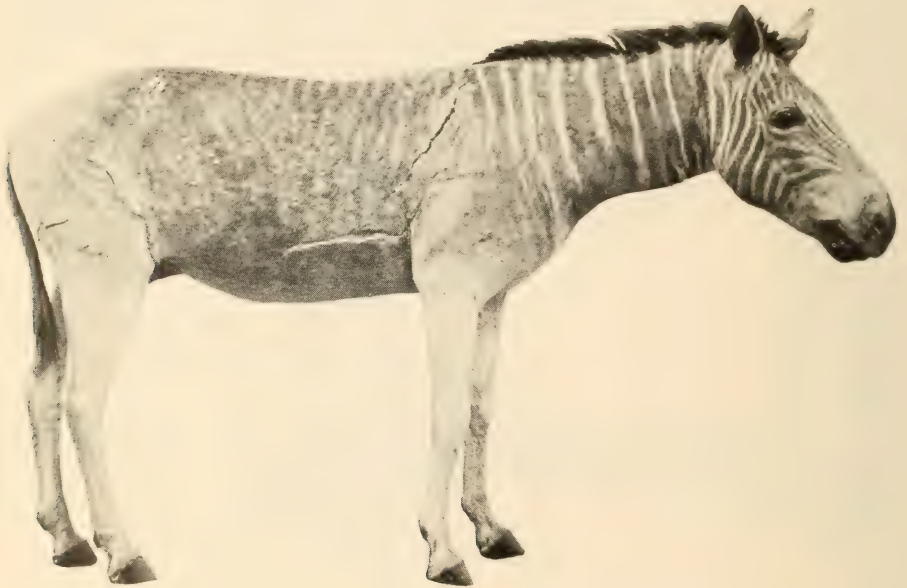


FIG. 16. Munich quagga.

Catalogue number: AM 541

Sex: female

Locality: —

Date of acquisition: 1834-5

Remarks on acquisition: bought from C. F. Ecklon, Hamburg, probably as unmounted skin

History of mount: mounted or remounted during first decade of this century by Inspector Küsthardt

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe not interrupted; most of ventral median stripe lost through taxidermy

Measurements: head-body: 2,32 m
tail: 0,42 m
ear: 0,16 m
hindfoot: 0,46 m
shoulder height: 1,17 m

State of preservation: much cracked; specimen very light, probably faded

Further material of same individual: upper and lower incisivae in collection

Remarks: not exhibited

References: Wagner (1835); Renshaw (1904); Ridgeway (1909); Hilzheimer (1912); Antonius (1931, 1951)

MUNICH—skull

Catalogue number: AM 541a

Sex: female

Locality: —

Date of acquisition: 1834–5

Remarks on acquisition: bought from C. F. Ecklon, Hamburg, together with skin

State of preservation: occipital missing

Further material of same individual: —

References: Hilzheimer (1912)

MUNICH—upper and lower incisivae

Catalogue number: AM 561

Sex: male

Locality: —

Remarks on acquisition: —

Further material of same individual: —

NEW HAVEN—skeleton

Catalogue number: Osteology 1623 (490)

Sex: female

Locality: given as 'Syria (?)'

Date of acquisition: 1873

Remarks on acquisition: bought by O. C. Marsh from Edw. Gerrard, London;
of same animal as mounted skin at Edinburgh

State of preservation: some molars missing

Remarks: not articulated, cleaned 1923

References: Willoughby (1966)

PARIS—mounted skin and skeleton



FIG. 17. Paris quagga.

Catalogue number: not registered

Sex: male

Locality: Cape Colony

Date of acquisition: probably 1798

Remarks on acquisition: animal arrived at the Gardens of the King at Versailles in 1784 from the Cape Colony; was transferred to Paris (Jardin des Plantes) in 1793 or 1794 (Dorst 1952)

History of mount: original mount, mainly of wood

Description of striking features: face clearly striped; mane short; sudden change from dorsal colour to leg colour at elbow; light flanking bands of dorsal

median stripe not interrupted; tail brush very long (0,49 m beyond tip of tail), most probably not original as fixing on to tail can be seen; skin of chestnuts on front legs replaced by white-haired skin

Measurements: head-body: 1,93 m
tail: 0,29 m
ear: 0,15 m
hindfoot: 0,43 m
shoulder height: 1,18 m

State of preservation: good

Further material of same individual: there is an articulated skeleton (No A544) labelled 'Quagga' in the Department of Comparative Anatomy, Paris Museum. It is not certain whether it belongs to the skin.

Remarks: not exhibited, stored in glass case

References: Desmarest (1820); Renshaw (1904); Trouessart (1906); Pocock (1907); Ridgeway (1909); Griffini (1913); Antonius (1931); Dorst (1952)

PHILADELPHIA—skeleton

Catalogue number: ANS 6317

Sex: male

Locality: —

Date of acquisition: 1898

Remarks on acquisition: donated by Professor E. D. Cope

References: Renshaw (1904)

PRETORIA—skull

Catalogue number: TM 10161

Sex: female

Locality: —

Date of acquisition: 'long ago'

Remarks on acquisition: identified in old collection by Lundholm

State of preservation: complete

References: Lundholm (1951)

STOCKHOLM—mounted skin



FIG. 18. Stockholm quagga foetus.

Catalogue number: Mam Ex. 14

Sex: foetus

Locality: Cape Colony

Date of acquisition: 1775

Remarks on acquisition: brought to Sweden by A. Sparrman

History of mount: original mount of straw; repairs with two hand-sized white leather patches might be of later date

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe not interrupted; interspaces fairly wide

Measurements:

head-body:	1,020 m
tail:	0,171 m
ear:	0,074 m
hindfoot:	0,230 m
shoulder height:	0,520 m

State of preservation: fair, mane almost lost

Further material of same individual: —

Remarks: a good painting of specimen was made about 1908 by S. Ekblom

References: Renshaw (1904); Ridgeway (1909); Lönnberg (1910); Antonius (1931)

STUTT GART—skull

Catalogue number: 16884

Sex: female

Locality: —

Date of acquisition: 1827

Remarks on acquisition: donated by Baron C. F. H. von Ludwig of Cape Town, probably belonging to skin which was sent to Darmstadt in 1830

State of preservation: complete

References: Hilzheimer (1912); Antonius (1951); Sheer *in lit.* (1959)

TRING—mounted skin



FIG. 19. Tring quagga.

Catalogue number: 394830

Sex: appears to be female; two large nipples present, vulva skin forming hump

Locality: —

Date of acquisition: 1889

Remarks on acquisition: bought by Lord Rothschild from Edw. Gerrard, London

History of mount: re-mounted by Edw. Gerrard before 1889

Description of striking features: face fairly striped; light flanking bands of dorsal median stripe much interrupted; ventral median stripe starting at last neck stripe

Measurements: head-body: 2,37 m
tail: 0,37 m
ear: 0,18 m
hindfoot, left: 0,48 m
hindfoot, right: 0,47 m
shoulder height: 1,19 m

State of preservation: good

Further material of same individual: skeleton was mounted at Amsterdam in 1855—now lost (Tuijn 1966)

Remarks: exhibited

References: Sclater (1901); Pocock (1904); Ridgeway (1909); Griffini (1913); Antonius (1931); Tuijn (1966)

TÜBINGEN—skull

Catalogue number: 488

Sex: male

Locality: —

Date of acquisition: 1842–50

Remarks on acquisition: Baron C. F. H. von Ludwig sent a quagga from South Africa to Tübingen in 1827 (Hilzheimer 1912)

State of preservation: occipital region missing

Remarks: The female quagga skull at Stuttgart is catalogued as: '1827 Von Ludwig, Kapkolonie' which leaves the origin of the Tübingen skull unknown, although it may possibly be one of the two quaggas formerly in the menagerie of Friedrich I, King of Württemberg

TURIN—mounted skin and skull

Catalogue number: 295?

Sex: female

Locality: —

Date of acquisition: 1827

Remarks on acquisition: specimen bought from dealer S. Leadbeater, London; it is possible that this is the first of the three quaggas received by the Rijksmuseum van Natuurlijke Historie at Leiden between 1827 and 1833 from their agent at Cape Town, Dr H. B. van Horstok

History of mount: original mount with several old repairs especially on head and lumbar region

Description of striking features: face clearly striped; light flanking bands of dorsal median stripe, where visible, not interrupted



FIG. 20. Turin quagga.

Measurements: head-body: 2,45 m
tail: 0,47 m
ear: 0,17 m
hindfoot: 0,49 m
shoulder height: 1,19 m

State of preservation: fair, rather dirty, with rusty patches on legs

Further material of same individual: skull (No 295) in collection

Remarks: not exhibited; stored in glass case

References: Camerano (1902, 1908); Renshaw (1904); Ridgeway (1909); Hilzheimer (1912)

VIENNA—mounted skin

Catalogue number: NMW—St. 710 (old number 1834/II/10)

Sex: female

Locality: —

Date of acquisition: April 1834

Remarks on acquisition: bought from C. F. Ecklon, Hamburg; Ecklon is known mainly for collecting botanical specimens in the Cape Colony, from where he returned to Hamburg several times

History of mount: original mount, like Paris specimen, mainly of wood

Description of striking features: specimen is the biggest of all preserved skins and obviously stretched as can be seen from the unusual width of both dorsal and ventral median stripes. Face clearly striped; light flanking bands of dorsal median stripe indicated only in anterior portion; in lumbar region light dots unite to form irregular continuous bands; stripe fragments below fork of shoulder stripe; body extensively striped; hair from striped areas with light and dark transverse sections



FIG. 21. Vienna quagga.

Measurements: head-body: 2,490 m
tail: 0,420 m
ear: 0,185 m
hindfoot, left: 0,510 m
hindfoot, right: 0,530 m
shoulder height: 1,260 m

State of preservation: good, fading noticeable on left side of head and neck

Further material of same individual: —

Remarks: not exhibited

References: Lorenz (1902); Renshaw (1904); Lydekker (1904); Ridgeway (1909); Griffini (1913); Antonius (1931)

WIESBADEN—mounted skin



FIG. 22. Wiesbaden quagga.

Catalogue number: 442

Sex: male

Locality: —

Date of acquisition: 1865

Remarks on acquisition: bought from dealer Frank, Amsterdam; probably third London Zoo quagga (Sclater 1901)

History of mount: original mount

Description of striking features: face faintly striped; body stripes with light dots; dorsal portion of body striping continuing transversely almost to root of tail, resembling gridiron pattern of *Equus zebra*; light flanking bands of dorsal median stripe sometimes slightly interrupted; tail-brush thick and very long; upper edge of hooves covered with long hair

Measurements: head-body: 2,30 m
tail: 0,41 m
ear: 0,16 m
hindfoot: 0,49 m
shoulder height: 1,20 m

State of preservation: fair; shrinkage has caused the opening of seams and several cracks in the skin, especially of the right side.

Further material of same individual: it is considered that the skeleton at the British Museum (Natural History), London, belongs to this individual

Remarks: exhibited

References: Anon (1858); Ridgeway (1909); Hilzheimer (1912); Antonius (1931)



FIG. 23. Doncaster; apparent quagga-hybrid foal.

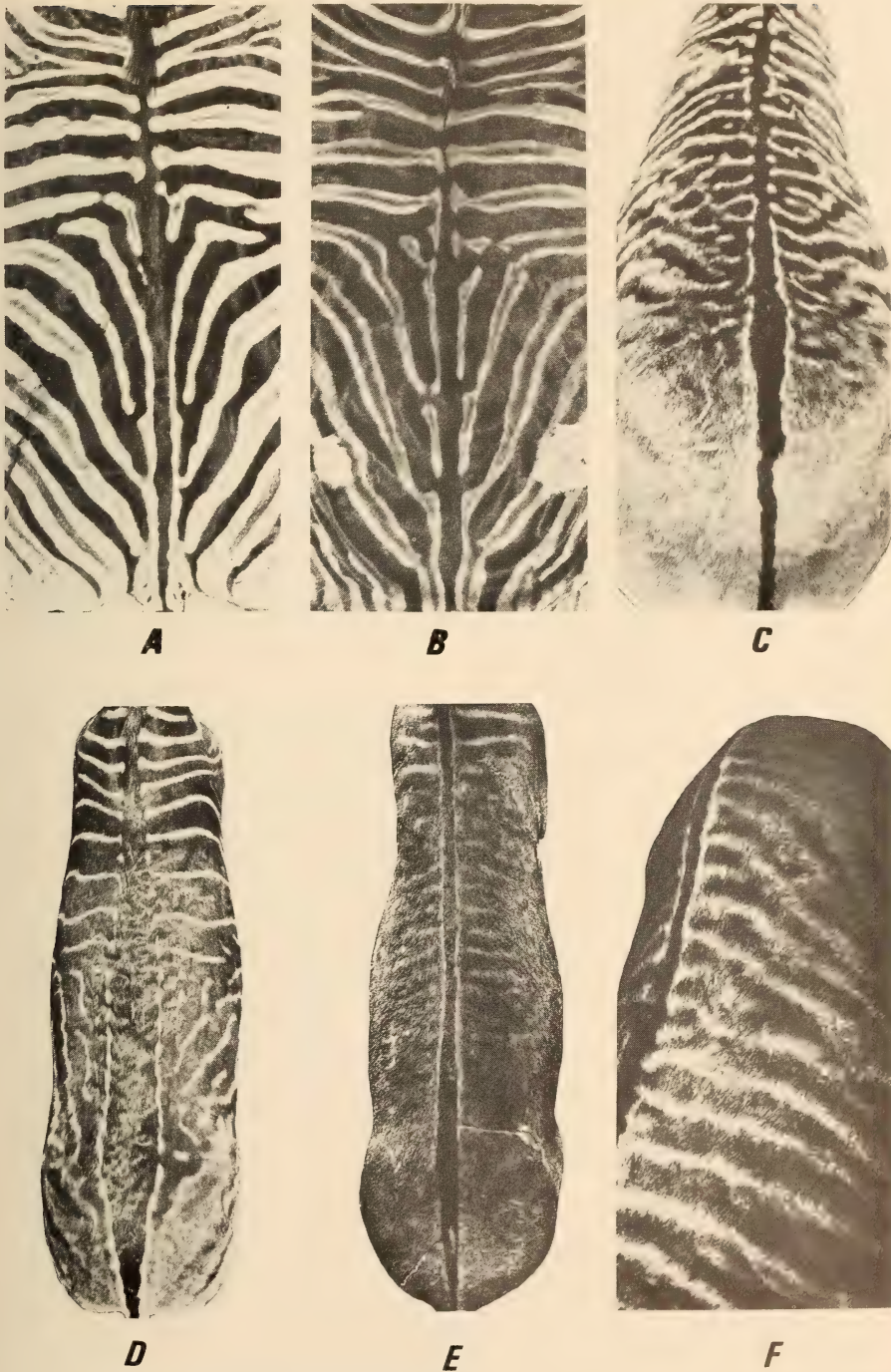


FIG. 24. Dorsal patterns of: A & B. Plains zebras from Zululand; note narrow anterior portion of dorsal median stripe and its indicated flanking bands. C. Tring quagga; note broader median stripe and its intensified flanking bands. D. Vienna quagga; animal appears stretched through taxidermy, which accounts for the excessive width of the dorsal median stripe; flanking bands further intensified. E. Munich quagga; note the continuous flanking bands. F. Wiesbaden quagga; note unusual extent of transverse stripes on rump.



FIG. 25. Successive decrease of stripes in members of the plains zebra group; from left, Cape Town quagga foal, Mainz male quagga; Mainz female Burchell's zebra; three plains zebras in Zululand; two East African plains zebras at Berlin Zoo.

ERRATUM

FIG. 25. To read: Successive increase . . .

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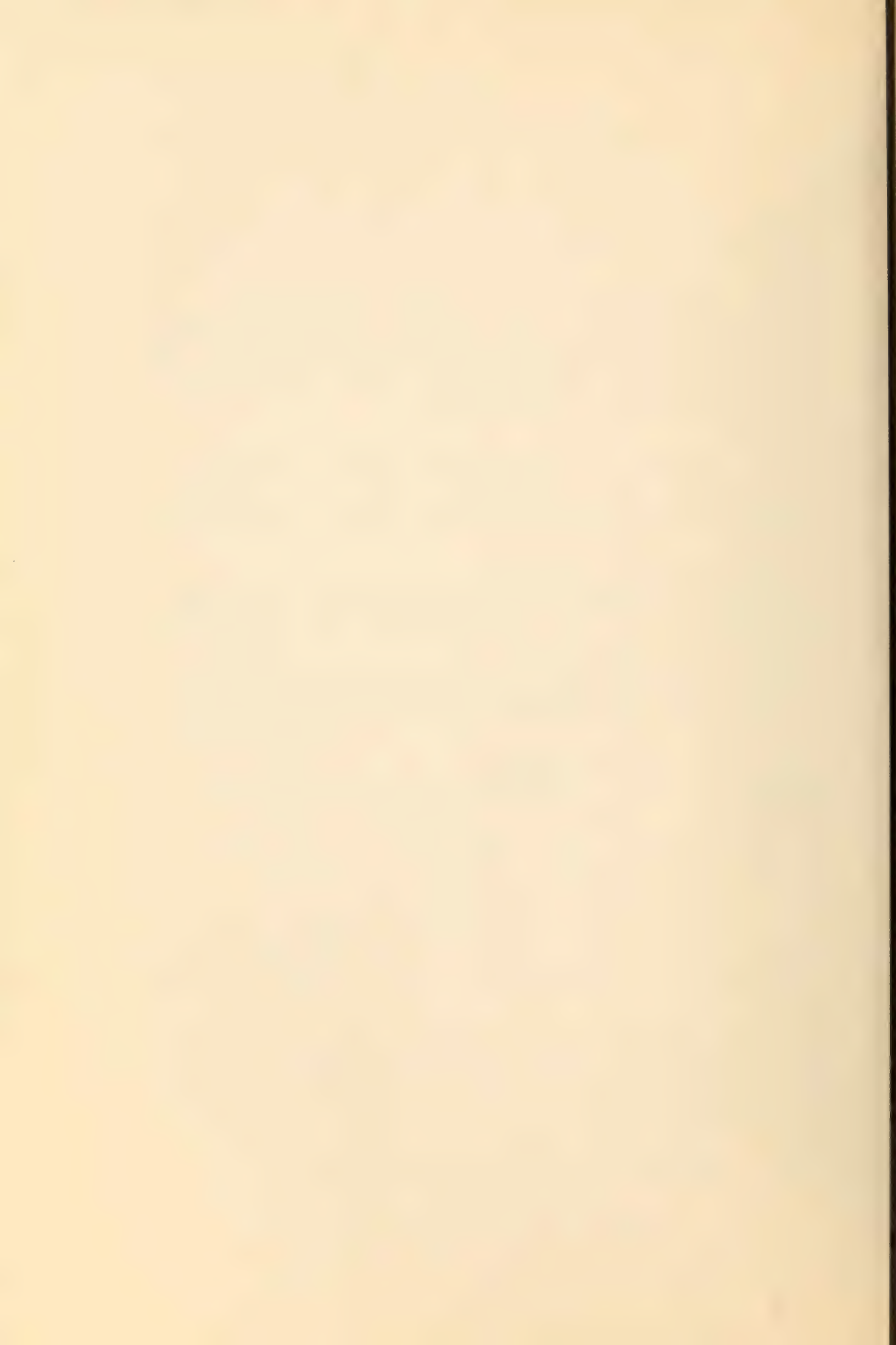
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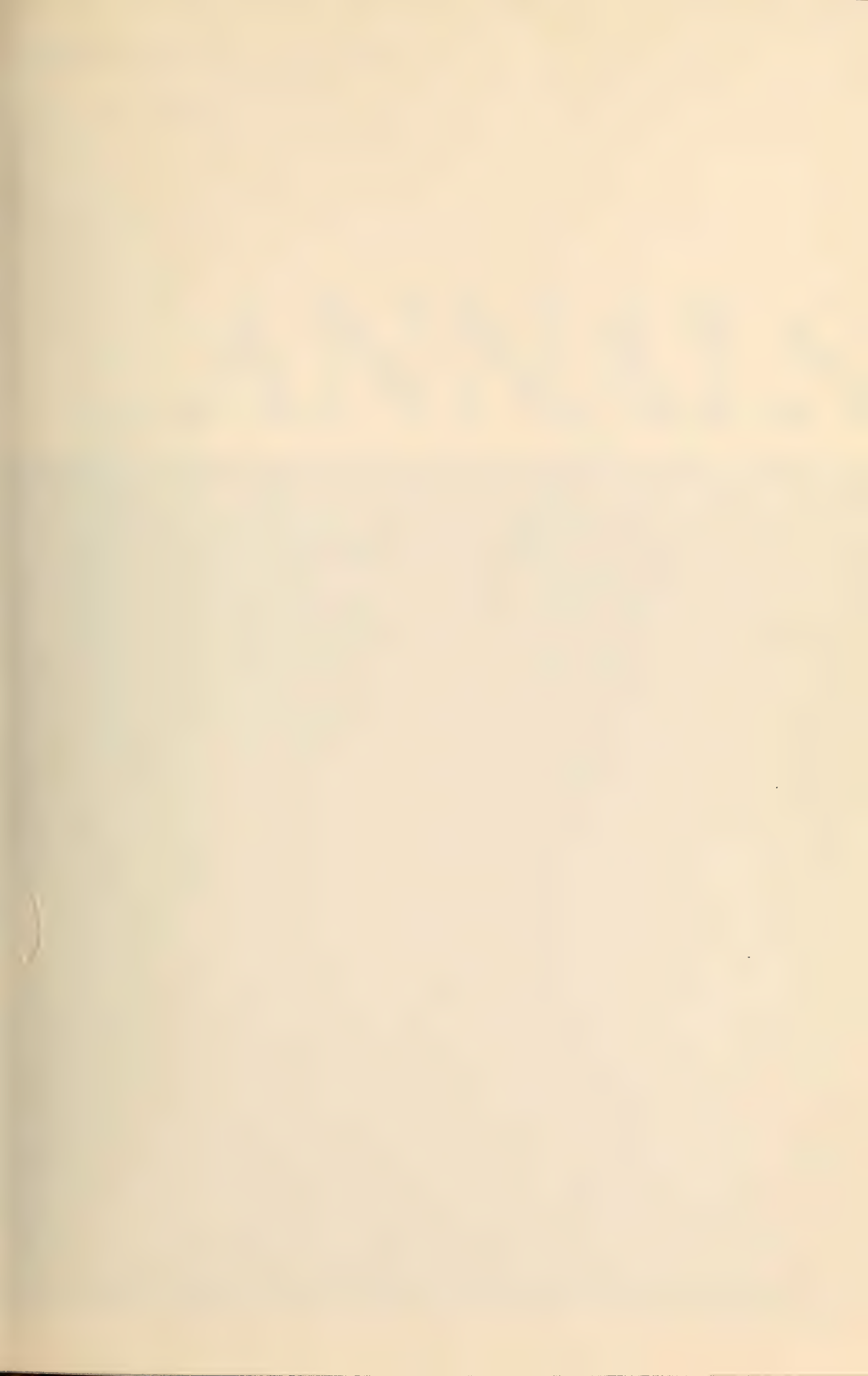
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R. E. Rau

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(COPEPODA, CALANOIDA)
FROM SOUTH AFRICAN ESTUARIES

By
ALLAN D. CONNELL
&
JOHN R. GRINDLEY

Cape Town Kaapstad

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TWO NEW SPECIES OF *ACARTIA* (COPEPODA, CALANOIDA) FROM SOUTH AFRICAN ESTUARIES

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Port Elizabeth Museum, Humewood, Port Elizabeth, South Africa

(With 27 figures and 1 table)

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INTRODUCTION

During studies of the zooplankton of South African estuaries two species of *Acartia* new to science have been found. One species, referable to the subgenus *Acartiella*, is often the numerically dominant copepod in estuaries on the east coast of southern Africa. The other species, of the subgenus *Paracartia*, occurs in estuaries on the east coast of South Africa, usually in smaller numbers although it is abundant occasionally. *Acartiella* and *Paracartia* are here regarded as subgenera (cf. Wellershaus 1969) despite Gurney's (1931: 217) proposal to remove them from *Acartia*. Bowman (1965: 149) pointed out that Steuer's (1915, 1923) primary division into '*Acartiae arostratae*' and '*Acartiae rostratae*' was unacceptable although his subgenera may be maintained.

DESCRIPTION OF MATERIAL

Acartia (Acartiella) natalensis sp. nov.

Figs 1-12, 24, 25

Material examined

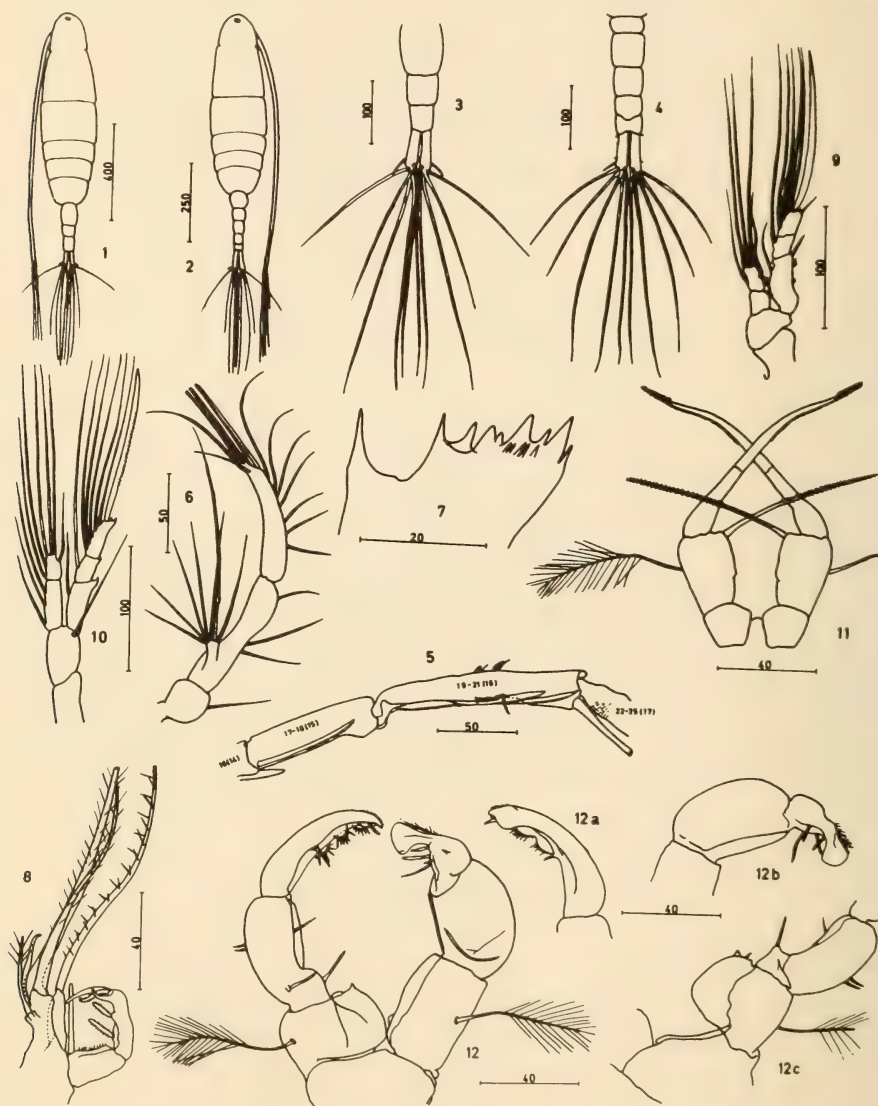
Numerous specimens in samples from estuaries between Knysna (34°S) and the Morumbene estuary, Mozambique (23°S).

Types

Holotype male (Reg. No. SAM A13408), allotype female (Reg. No. SAM A13409) and paratypes 10♂♂, 10♀♀ (Reg. No. SAM A13410) deposited in the South African Museum, Cape Town, from the Mtentu River estuary (31°14,5'S, 30°2'E) on the Pondoland coast of South Africa.

*Description**Female* (Figs 1, 3, 6-9, 11)

Total length 0,93 to 1,05 mm (Morrumbene specimens were considerably smaller: 0,87 to 0,90 mm, and Knysna specimens were also smaller: 0,82 to



Figs 1-12. *Acartia (Acartiella) natalensis* sp. nov. 1, female dorsal view; 2, male, dorsal view; 3, female, urosome, dorsal view; 4, same, male; 5, geniculate portion of male right first antenna; 6, female, second antenna; 7, female, mandible; 8, female, maxilliped; 9, first leg, female; 10, male, fourth leg; 11, female, fifth leg; 12, male, fifth leg (posterior view); 12a, 12c, anterior view, right leg; 12b, anterior view, left leg. All measurements in microns.

0.90 mm). The head is slightly produced anteriorly. No rostrum or filaments are present. The postero-lateral corners of the prosome are spineless (Fig. 1). The first antennae reach the posterior end of the furcal rami. Urosome segments are devoid of spines (Fig. 3), but the anal segment usually bears a single transverse row of minute hairs on its dorsal surface. The furcal rami each bear five long plumose setae, four terminal and one dorsal, and a short curved accessory seta laterally about twice as long as ramal width. The furcal rami are asymmetrical, the right being longer.

The first antennae consist of 22 apparent segments, but 'segment' 2 is apparently compounded of 3 segments and 'segment' 4 of 2, giving 25 true segments. Segments 13 to 20 (apparently 10 to 17) have a row of small spines, slightly less in length than the width of the segments. Segment 22 is only fractionally longer than wide.

The second antennae are somewhat atypical for the subgenus, being of the normal *Acartia* form (Fig. 6), and apparently resembling those of *A. (Acartiella) kempi* (Sewell, 1914), the only other described member of the subgenus with this type of second antenna. The endopod is relatively small. There are no hairs on the inner margin of the exopod. There are slight differences in setation in specimens from different localities.

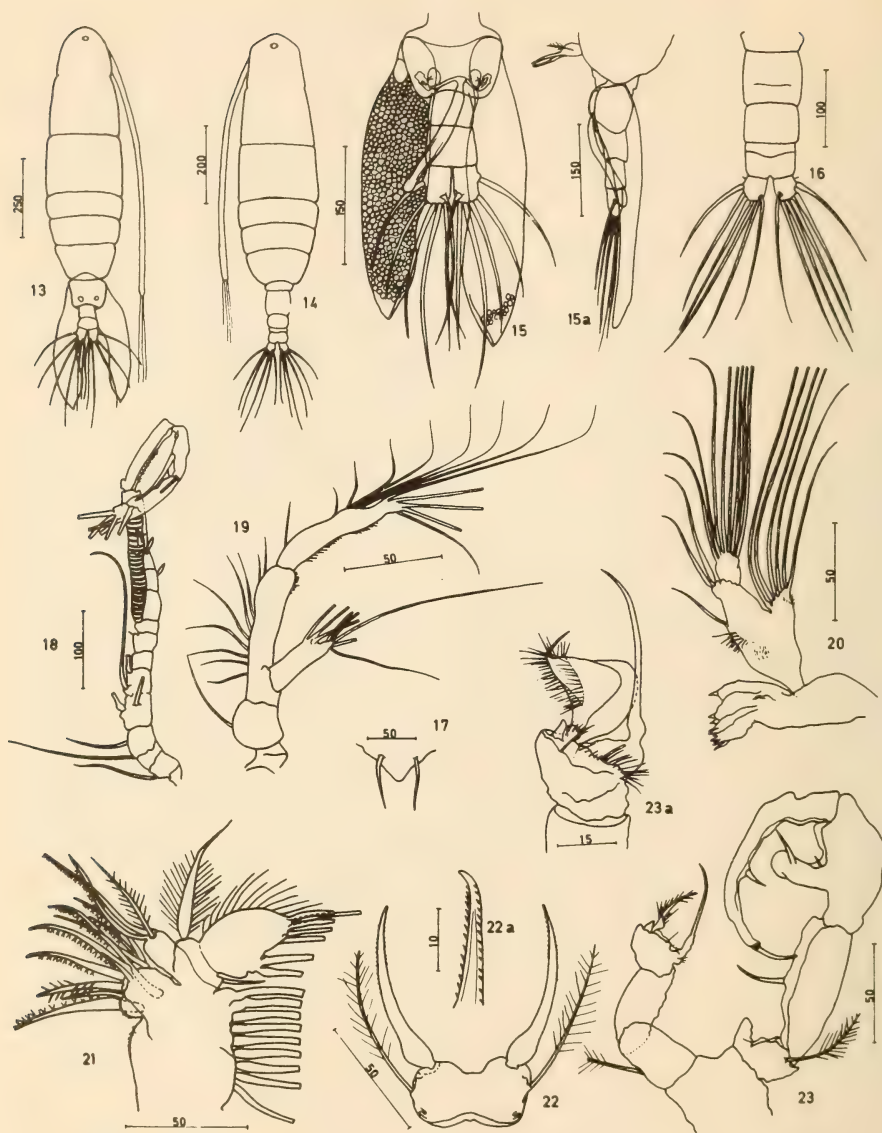
The first maxilla has the base more expanded than in that of *A. (Paracartia) longipatella* sp. nov. (Fig. 21) and lacking the patches of fine setae on the inner margin. There are no hairs on the distal margin of the exopod.

The second maxillae are normal, bearing approximately 15 setae of varying length. The maxillipeds are as figured (Fig. 8) with three strong and two reduced biplumose setae on the basal segment. Specimens from Knysna show these five setae more equally developed. The four pairs of swimming legs are typical of the genus (Table 1). On the first leg the second segment of the exopod, however, lacks the outer marginal spine on its apical angle (Fig. 9), while this spine is present but much reduced on legs 2 to 4. This spine is barely noticeable in legs 2 and 3 in many specimens. Leg 5 is distinctive from that of all other known species of the subgenus *Acartiella*. The exopod is basally about four times thicker than the endopod (Fig. 11), while the endopod is $\frac{3}{4}$ as long as the exopod, bearing short hairs as figured. There is no seta midway on the outer margin of the exopod.

Male (Figs 2, 4, 5, 10, 12, 24, 25)

Total length 0.82–0.88 mm (Morrumbene specimens 0.76–0.79 mm, Knysna specimens 0.73–0.78 mm). General shape is similar to the female although the urosome is longer relative to the prosome length (Fig. 2). The last urosome segment has a couple of small spines, and there are usually two or three on the outer edge of the caudal rami (Fig. 4). Only the left ramus has a short curved accessory seta, while the plumose setae are similar to those of the female.

The first antennae extend to the distal end of the furcal rami. The left antenna is as in the female, while the right has only 17 apparent 'segments',



Figs 13–23. *Acartia (Paracartia) longipatella* sp. nov. 13, female, dorsal view; 14, male, dorsal view; 15, female, urosome, semi-schematic, showing position of accompanying plates; 15a, same, lateral view; 16, dorsal view male urosome; 17, female, rostrum, and filaments; 18, male, right first antenna; 19, male, second antenna; 20, male, mandible and palp; 21, female, first maxilla; 22, female, fifth leg; 23, male fifth leg, anterior view; 23a, another detailed view of the left fifth leg. All measurements in microns.

TABLE 1

Ornamentation of the swimming legs of *Acartia* (*Acartiella*) *natalensis* sp. nov.
Si, Se, St represent internal, external and terminal spines or setae respectively.
The number of setae is shown in arabic numerals and spines in roman numerals.

Leg	Protopod				Endopod				Exopod							
	1		2		1		2		1		2		3			
	Si	Se	Si	Se	Si	Se	Si	St	Se	Si	Se	Si	Se	Si	St	Se
P ₁	0	0	0	0	0	0	2	2	1	1	I	1	0	4	I	I
P ₂	0	0	0	0	2	0	4	2	1	1	I	1	I*	5	I	I
P ₃	0	0	0	0	2	0	4	2	1	1	I	1	I**	5	I	I
P ₄	0	0	0	1	3	0	3	2	1	1	I	1	I**	5	I	I

* much reduced

** reduced

several of them compound. The geniculation is between 'segments' 15 and 16 these being compounds of true segments 17-18 and 19-21 respectively (Fig. 5). Apparent segment 9 bears a short heavy spine, while 10 and 11 are swollen. 'Segments' 14, 15 and 16 bear serrated, sabre-like spines (Fig. 5).

The remaining appendages from the second antenna to leg 4 are as in the female.

The male 5th legs differ markedly from those of other members of the subgenus (Figs 12, 12a, 12b, 12c, 24, 25). The right leg does however form a well-developed clasping apparatus as specified by Sewell (1914) in his definition of the subgenus. The detail of the terminal structures of P5 left segment 2-3 was difficult to determine clearly and was therefore photographed under the scanning electron microscope after critical-point drying (Figs 24, 25).

Occurrence

This species was abundant in most estuaries on the east coast of southern Africa between Knysna and Morumbene. It was collected in waters of varying salinity from 3.3 to 65‰.

Discussion

Although the shape of the second antenna places this species with *kempi* Sewell, 1914, the male and female 5th legs are unusual and somewhat different from any known species. The key to *Acartiella* species provided by Wellershaus (1969) (from which *A. sinensis* Chia-jui & Foo-siang, 1963 is omitted) easily accommodates *natalensis*, since this species is easily distinguished from *kempi* by the structure of the 5th leg of both male and female.



Figs 24–25. *A. (Acartiella) natalensis* sp. nov. Male fifth leg, left, 1, lateral view, 2, dorsal view (with some debris caught in the setae).



Figs 26–27 *A. (Paracartia) longipatella* sp. nov. Male fifth leg, left, lateral view.

This species is one of the dominant copepods at least as far north as the Morumbene estuary, suggesting a wider distribution probably extending to estuarine waters of the east African coast. Its presence in South African waters considerably increases the known range of the subgenus *Acartiella*, previously confined to Indian, Burmese and south Chinese coastal and estuarine waters.

Acartia (Paracartia) longipatella sp. nov.

Figs 13–23, 26, 27

Material examined

Many specimens in samples from estuaries from between the Klein River estuary (Hermanus) and St. Lucia (Natal). It was not observed in samples from Mozambique estuaries or from estuaries on the west coast of South Africa.

Types

Holotype male (Reg. No. SAM A13411), allotype female (Reg. No. SAM A13412) and paratypes 10♂♂, 10♀♀ (Reg. No. SAM A13413) deposited in the South African Museum, Cape Town, from the Mtentu River estuary (31°14.5'S, 30°2'E) on the Pondoland coast of South Africa.

Description

Female (Figs 13, 15, 17, 21, 22)

Total length 0.98–1.04 mm (Knysna specimens 0.80–0.88 mm, Breede River specimens 0.82–0.90 mm). The head is slightly produced anteriorly. A rostrum and filaments are present (Fig. 17). The postero-lateral corners of the prosome are rounded (Fig. 13), with the first urosome segment greatly enlarged, the posterior two segments normal (Fig. 15). The caudal rami are short, only slightly longer than wide. Caudal setae are as figured (Fig. 15). On mated females the accompanying plates (Sars 1904) of the spermatophore reach far past the posterior tip of the furcal rami (Fig. 15).

The first antennae reach almost to the posterior end of the first urosome segment (Fig. 13), with 19 recognizable segments. The second antennae are of the normal *Acartia* form, with fine setae on the inner margin of the exopod and second basal segment (Fig. 19). The mandible with its palp is as figured for the male (Fig. 20). The first maxilla is figured (Fig. 21). The second maxilla is typical of the genus, bearing approximately fifteen setae of varying length. The maxilliped is similar to that figured for *A. (Acartiella) natalensis* (Fig. 8), but the second segment is more swollen and has its plumose spine much shorter than that of *A. natalensis*.

The first swimming leg is similar to that of *A. natalensis* (Fig. 9) but has an outer marginal spine on the apical angle of each of the three exopod segments, while segment 3 has, in addition, a median external seta and a short spine near the base of the terminal spine. The setal formula of the inner margin of the

endopod segments is 1:3 compared with 0:2 of *A. natalensis* (Fig. 9 and Table 1). Legs 2-4 are similar to *A. natalensis* (Fig. 10), but a short stout spine is well developed on all 3 segments of the exopod.

The female fifth legs resemble those of other *Paracartia* species, but the outer plumose setae are subequal in length to the exopods (Fig. 22), which are not as strongly curved as those of *P. africana* (Steuer).

Male (Figs 14, 16, 18-20, 23, 26, 27)

Total length 0,82-0,88 mm (Knysna specimens 0,76-0,87 mm, Breede River specimens 0,75-0,79 mm). The head is rather more truncate anteriorly. The last segment of the prosome has rounded postero-lateral corners (Fig. 14). Urosome segments are not greatly enlarged. The furcal rami are no longer than their width. Setae are as illustrated (Fig. 16).

The first antennae reach to the posterior margin of the prosome (Fig. 14). The left antenna is as described for the female, the right is as figured (Fig. 18), and the geniculation is between the fourteenth and fifteenth 'segments', the fourteenth bearing a stout, blunt spine slightly longer than segment length. 'Segments' 9-13 are hollowed anterodorsally.

The appendages from second antenna to fourth leg are as for the female. The right fifth leg is greatly enlarged (Fig. 23), and is typical of males of the subgenus *Paracartia* (see Steuer 1923). The left side is also fairly typical, being somewhat reduced. The terminalia include a long thin spine and a broader plate, setose along one edge (Figs 23, 23a). The line-drawings were confirmed by scanning electron microscope photographs (Figs 26, 27).

Occurrence

This species was present in estuaries between Hermanus (Klein River estuary) and Natal (St. Lucia), usually in small numbers but occasionally abundant. It was obtained in waters of varying salinity from 7-35,5‰.

Discussion

There are only four members of the subgenus previously described and their distribution ranges down the east side of the Atlantic Ocean, with *P. latisetosa* (Kriczagin) penetrating into the Mediterranean and Black Seas. The most northerly species is *P. grani* Sars, from the north-west coast of Europe (Sars 1904), while *P. dubia* Th. Scott has been collected in the Gulf of Guinea and *P. africana* along the South West African coast (Unterüberbacher 1964) and west coast of South Africa (unpublished record).

Acartia asymmetrica Tanaka, 1964, described from the 'Bay of Cape Town' is a synonym of *Acartia* (*Paracartia*) *africana* Steuer.

The occurrence of a member of the subgenus in east coast temperate and subtropical estuaries is thus interesting, and extends the range of the subgenus into the Indian Ocean.

The lack of any form of wing-like projection on the last prosome segment

in the female is distinctive, as is the shape of the first urosome segment and the size and shape of the spermatophore plates, in mature females. The prominence of these long plates gives rise to the name proposed for this species.

Both *Acartia (Acartiella) natalensis* and *Acartia (Paracartia) longipatella* appear to be restricted to estuaries and neither species has been found in the open sea.

SUMMARY

Two new species of *Acartia* are described from estuaries on the east coast of southern Africa. *Acartia (Acartiella) natalensis* occurs in estuaries in South Africa and Mozambique, while *Acartia (Paracartia) longipatella* has only been recorded from estuaries on the east coast of South Africa.

ACKNOWLEDGEMENTS

We thank Mr T. R. Wooldridge and Mr A. F. de Villiers for assistance with the examination of specimens. We gratefully acknowledge that Dr A. de Decker of the Division of Sea Fisheries also recognized these two species as undescribed but left their description to us.

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

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KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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(COPEPODA, CALANOIDA)
FROM SOUTH AFRICAN ESTUARIES

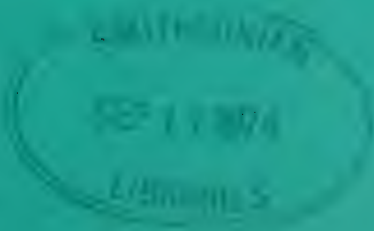
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ON THE TAXONOMIC STATUS, DISTRIBUTION
AND ECOLOGY OF THE BLUE ANTELOPE,
HIPPOTRAGUS LEUCOPHAEUS (PALLAS, 1766)

By
RICHARD G. KLEIN

Cape Town Kaapstad

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THE BLUE ANTELOPE, *HIPPOTRAGUS LEUCOPHAEUS*
(PALLAS, 1766)

By

RICHARD G. KLEIN

Department of Anthropology, University of Chicago, Chicago

(With 2 figures, 1 map and 3 tables)

[MS. accepted 10 July 1973]

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INTRODUCTION

The first published account of the blue antelope was made by the German Peter Kolb (1719 as cited in Mohr 1967: 6-10) who lived and travelled in what is now known as the south-western and southern Cape between 1705 and 1712. Subsequently, other nineteenth-century visitors to the Cape published independent descriptions of this creature, which they encountered just east of the Hottentots-Holland Mountains, mainly in the triangle Swellendam-Caledon-Bredasdorp but occasionally as far east as Plettenberg Bay. On the basis of skins and skulls sent back to Europe, Pallas (1766 as cited in Mohr 1967: 11) presented the first truly systematic description of the species, which he called *Antilope leucophaea*. In 1774 Thunberg reported that the blue antelope had become very uncommon (Mohr 1967: 6). The last one was seen around 1800, making this species the first historically recorded African mammal to become extinct (Harper 1945: 698-700).

The early extinction of the blue antelope, before qualified scientists could observe wild or even captive specimens, left open many questions concerning its

physical appearance, taxonomic status, geographic distribution, and ecology. There are, of course, no photographs, and most of the available sketches and descriptions are obviously inaccurate in one respect or another. Kolb, for example, drew the creature with a beard, apparently because he thought it was a close relative of the goats (he placed the blue antelope in the genus *Capra*) and some subsequent writers followed this custom. From Mohr's (1967) review of the early drawings and descriptions, it is apparent that they often contradict one another and are also at variance with the four mounted specimens still available in Europe, as well as with what may be surmised about the blue antelope from knowledge of its closest living relatives, the roan (*Hippotragus equinus*) and the sable (*H. niger*).

In her monographic study of the blue antelope, Mohr (1967) was forced to rely heavily on the mounted specimens (one each in Vienna, Stockholm, Paris, and Leiden) and on a skull housed in the Hunterian Museum at the University of Glasgow. This skull has no history attached to it, but Broom (1949) assigned it to *H. leucophaeus*, mainly because there was reason to believe it had been obtained before 1800—a time when the blue antelope was the only species of *Hippotragus* that had been encountered by Europeans (according to Broom, *H. equinus* was first seen by Europeans in 1804, *H. niger* in 1836). In the few years since Mohr's monograph was completed, a considerable amount of relevant osteological material has been found at archaeological and palaeontological localities in or near the area where *H. leucophaeus* was recorded historically. The purpose of this paper is to summarize the taxonomic, distributional, and ecological implications of this material.

DEFINITION OF THE SAMPLES

The initial stimulus for this paper was the observation that teeth assignable to the genus *Hippotragus* from the archaeological site of Nelson Bay Cave (Plettenberg Bay) were remarkably variable in size (Fig. 1), being sometimes significantly smaller and sometimes appreciably larger than homologous teeth of the largest *H. equinus* specimen in the South African Museum's comparative collection. Nelson Bay Cave lies within the historic area of distribution of *H. leucophaeus*, and it seemed highly probable that it would be represented at the site. With this in mind, two explanations of the observed size variation in Nelson Bay *Hippotragus* teeth seemed possible: (1) All the Nelson Bay teeth derived from *H. leucophaeus*, which was highly variable in size and which, contrary to historic observations, included some individuals as large or larger than the living roan; (2) the Nelson Bay sample included teeth from *H. leucophaeus* and

also from another species of *Hippotragus*, perhaps *H. equinus*.¹ In order to determine which hypothesis was more likely and possibly at the same time establish some of the metrical characteristics of *H. leucophaeus* vs. those of *H. equinus* and *H. niger*, it was obviously necessary to obtain measurements on samples of well-defined *H. equinus* and *H. niger* and also on fossil *Hippotragus* from other southern Cape sites.

A list of the relevant fossil sites with some background data on each is presented in Table 1. Map 1 gives their locations. At most of the sites, analysable *Hippotragus* remains consist overwhelmingly of isolated teeth. Whole dentitions are common only from Swartklip and even there the number is not large. Three sites have provided analysable horn cores (an example from Nelson Bay Cave is illustrated in Fig. 2). No complete or even nearly complete skulls are known. Post-cranial remains occur at several sites, but have been ignored here because: (1) they are exceedingly difficult to distinguish from the post-cranial bones of other similar-sized bovid genera represented in the same collections; (2) most of the post-cranial material is highly fragmentary, greatly reducing its descriptive and analytic value (and compounding the difficulty of generic identification); and (3) there are no large museum samples of well-identified recent *Hippotragus* post-cranial remains with which to compare the fossil material. Data on the quantities of analysable teeth and horn cores available from the different sites are presented in Appendix 1.

The recent samples of *H. equinus* and *H. niger* with which the fossil material is compared are composites of collections housed in the South African Museum (Cape Town), the Transvaal Museum (Pretoria), the National Museum of Rhodesia (Bulawayo), the British Museum (Natural History) (London) and the Field Museum of Natural History (Chicago). The geographic provenances of the samples are given in Table 2, from which it can be seen that specimens from south-central Africa (especially Zambia) predominate heavily in both samples, giving them a distinct geographic bias. There are two few well-provenanced specimens from other areas in either the *H. equinus* or the *H. niger* sample to say with any certainty that geographic differences in size do not characterize either or both species, but the data are sufficient to argue that any differences which do exist are probably small. Further, my search of the literature has failed to turn up any references to marked size differences among recognized subspecies of either *H. equinus* or *H. niger*, with the exception of *H. niger variani*, the 'giant sable' of Angola. I encountered only one *H. niger variani* specimen in the museum collections I examined (in the Field Museum) and measurements on it were recorded separately from those of the remaining *H. niger* sample. I think it is fair to conclude that the admitted geographic bias of the two comparative samples does not disqualify them for use in this study.

¹ The possibility that the second species might be the extinct giant hippotragine, *Hippotragus gigas*, was ruled out since the relevant Nelson Bay teeth were all morphologically quite distinct from teeth of *H. gigas*, as known, for example, from Elandsfontein. The dentition of *H. gigas*, in fact, is morphologically more like that of recent *Oryx* spp. (though much larger) than that of recent *Hippotragus* spp.

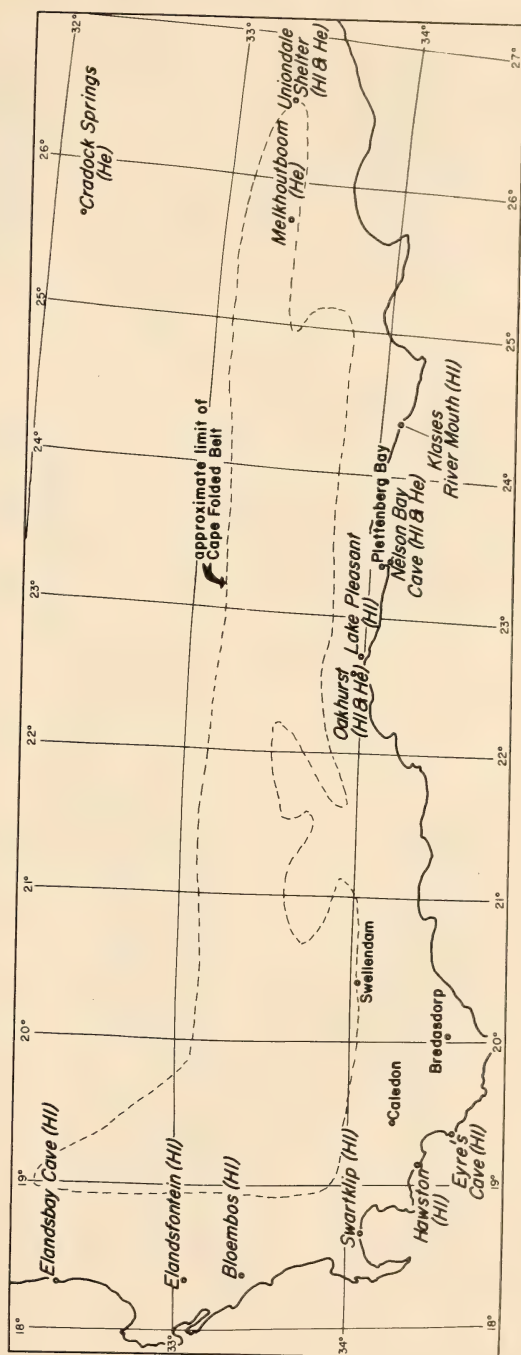
Table 1

Southern Cape palaeontological and archaeological sites from which the *Hippotragus* remains analysed in this paper were derived.

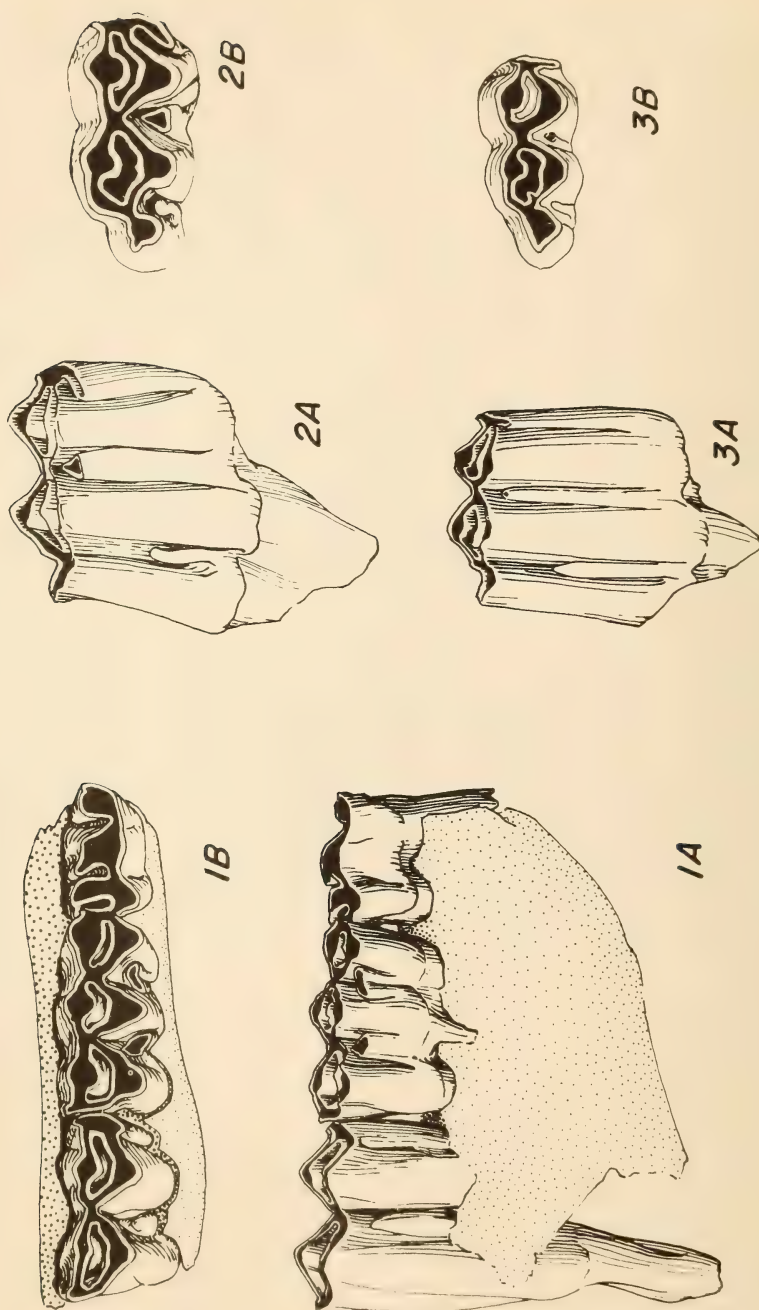
Site	Bone accumulation related to human activity?	Geological age of <i>Hippotragus</i> fossils (and nature of supporting evidence) ^a	Reference	Present location of material
Elands Bay Cave	Yes	11 000 to shortly after 9 600 B.P. (C-14)	Parkington (1972); Klein (unpubl.)	Department of Archaeology, University of Cape Town
Elandsfontein	Probably at least in part	Middle and Upper Pleistocene (palaeontological inference) ^b	Hendey (1969, 1974); Klein (1974)	South African Museum
Bloembos	Possibly	?Upper Pleistocene (palaeontological inference)	Cooke (1947); Hendey (1974)	South African Museum
Eyre's Cave	Probably	Later Last Glacial and Holocene (palaeontological and archaeological inference)	Klein (1974)	South African Museum
Hawston	Probably	?Holocene (no provenance data)	None	South African Museum
Oakhurst	Yes	Terminal Last Glacial and Holocene (archaeological inference)	Goodwin <i>et al.</i> (1938); Wells (1960)	South African Museum
Lake Pleasant (Groenvlei)	No	?Later Last Glacial (geological inference)	Butzer & Helgren (1972)	South African Museum
Nelson Bay Cave	Yes	18 500–5 000 B.P. (C-14) ^c	Klein (1972a, b, 1974)	South African Museum
Swartklip	No	>40 000 years B.P. ^d ; earlier Last Glacial (C-14 and geological inference)	Hendey & Hendey (1968); Butzer (in press)	South African Museum
Klasies River Mouth Caves	Yes	Between >30 000 B.P. and the end of the Last Interglacial (C-14 and geological inference)	Wymer & Singer (1972 and in press); Klein (1974)	South African Museum
Craddock Springs	Probably	Earlier Last Glacial (archaeological inference)	Wells (1970); Klein (1974)	Port Elizabeth Museum
Melkhoutboom	Yes	15 400 to shortly before 7 600 B.P. (C-14)	Deacon (1969, 1972)	Department of Archaeology, University of Stellenbosch
Uniondale Shelter	Yes	Holocene (archaeological inference)	M. Brooker (pers. comm.)	Albany Museum (Grahamstown)

NOTES:

- ^a The term Upper Pleistocene is used here to refer to the combined time-span of the Last (Eem) Interglacial and the Last (Würm) Glacial, or in absolute terms, roughly the time interval from 125 000 B.P. to 10 000 B.P. The Last Interglacial/Last Glacial boundary probably falls in the interval 75 000–70 000 B.P.
- ^b Most of the Elandsfontein faunal material has been collected from one or more calcareous or ferruginous palaeosurfaces exposed during recent deflation of overlying sands. The bulk of the fauna probably dates from the Middle Pleistocene (Klein 1974), but a portion, including perhaps bones assigned to *H. leucophaeus*, may be considerably younger.
- ^c Inskeep has excavated deposits at Nelson Bay that are younger than 5 000 B.P. These may also contain hippotragine remains, but the mamalian fauna from them has not yet been analysed.
- ^d A single C-14 date of >40 000 years. (1–6840) (Buckley, pers. comm.) has been obtained on ostrich eggshell in direct association with mammal bones at Swartklip.



Map. 1. Southern Cape localities mentioned in the text (HI, He—locality contains bones assigned to *Hippotragus leucophaeus* or *H. equinus* respectively).



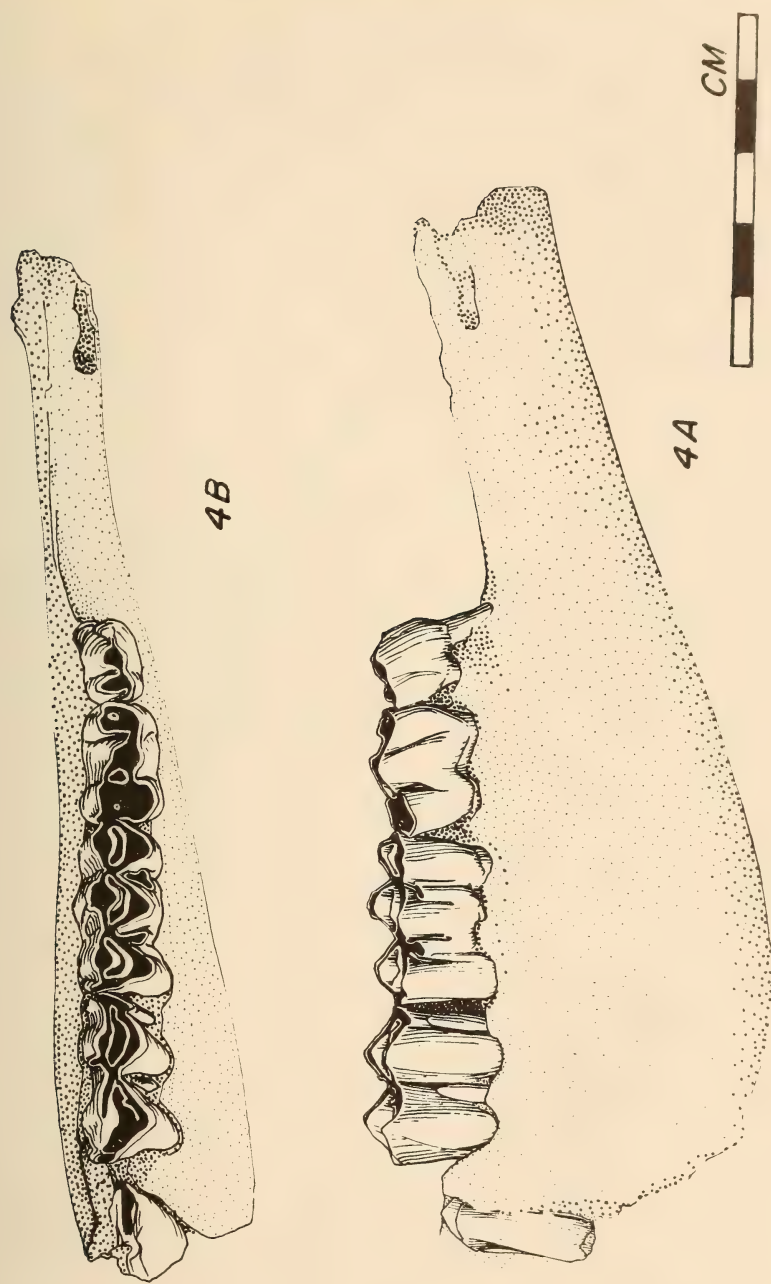


Fig. 1. 1A, 1B: dP_2 (MW), dP_2 (MW), M_1 (EW) of *Hippotragus equinus* from Nelson Bay Cave (SAM BSJ/4B1); 2A, 2B: M_3 (MW) of *H. equinus* from Nelson Bay Cave (SAM BSJ/94G7); 3A, 3B: M_3 (EW) of *H. leucophaeus* from Nelson Bay Cave (SAM CS/3B5); 4A, 4B: dP_2 (EW), dP_2 (MW), dP_4 (MW), M_1 (EW), M_2 (unruptured) of *H. leucophaeus* from Lake Pleasant (SAM Q1777). (Drawings by K. Scott.)

Table 2

Geographic origin of the comparative specimens of *Hippotragus* used in this study.

	NUMBER OF SPECIMENS		
	<i>H. equinus</i>	<i>H. niger</i> subsp.	<i>H. niger varians</i>
South Africa (Transvaal)	5	22	0
Swaziland	1	0	0
South West Africa	1	0	0
Botswana	1	2	0
Rhodesia	5	8	0
Zambia	45	31	0
Malawi	2	0	0
Angola	0	0	1
No provenance given in museum catalogues	39	19	0
TOTALS	99	82	1

DEFINITION OF THE MEASUREMENTS

The only dimension measured on both fossil and recent teeth was maximum length at the level of the occlusal surface, on the buccal side for maxillary teeth and on the lingual side for mandibular ones. Whenever possible (mainly on the comparative specimens), maximum length of whole premolar and molar rows were also recorded. The maximum length measurement has the dual advantage of analytic utility and easy definition and replication. Furthermore, it is the dental measurement most frequently used by other investigators of bovid fossils (see, for example, Gentry 1966 or 1970).

Casual observation is sufficient to show that the individual teeth, and especially the molars of *Hippotragus* spp., change length as they wear. In order to reduce sample variance and possible sample bias from this factor, four wear categories were defined and only measurements on homologous teeth in the same wear category are compared below, except in the case of whole molar and premolar rows where observation suggests there is relatively little length change with wear in any case (as some teeth grow shorter within a row, others become correspondingly longer). For the molars, the four wear categories are: (1) No Wear (NW)—no obvious wear on the molar crown; (2) Early Wear (EW)—wear on the crown obvious, but basal pillar not part of occlusal surface; (3) Medium Wear (MW)—basal pillar part of occlusal surface but tooth still characterized by considerable height above the alveolus (or on isolated teeth above the roots); and (4) Late Wear (LW)—tooth worn down to near the level of the alveolus (or, in the case of isolated teeth, to near the level of the roots, with occlusal surface very flat and smooth). The same four categories were used for the premolars (both deciduous and permanent), but are harder to define because, with the exception of dP₄, the premolars do not generally possess basal pillars. Separation of premolars in Early Wear and in Medium Wear is thus particularly difficult, but tests made to see whether the same tooth would be classified in the



Fig. 2. *Hippotragus leucophaeus*. Horn core from Nelson Bay Cave (SAM YGL 53/G3).

same wear category in successive weeks included no failures, suggesting that, however difficult to define, wear category judgements were at least consistent. In any case, the premolars do not change shape and length from Early Wear to Medium Wear as dramatically as the molars do so that confusion of premolar wear categories is unlikely to seriously affect any conclusions reached below.

Since most of the fossil horn cores lack the tip and sometimes a good part of the length adjacent to the tip, and since the sheaths could not be completely removed from many of the comparative specimens, horn-core measurements were restricted to the maximum longitudinal (antero-posterior) and transverse (medio-lateral) diameters immediately above the pedicel. These diameters are useful not only in themselves, but also because the ratio between them is a measure of transverse (side-to-side) compression. Thus, taken together, they may be used to say something about both the size and the shape of a basal horn-core cross-section. One difficulty in using the diameters to compare hippotragine species, however, is the fact that there are very great differences in basal horn-core size and shape between subadults and adults and between males and females within both *H. equinus* and *H. niger*. (In both species, young females have the smallest, most rounded horn-core bases, adult males the largest, most transversely compressed ones.) Sex is easy enough to take into account, but age is somewhat more difficult (for the teeth it is implicitly taken into account by the use of the wear categories). Since the bony consistency (solidity and non-porosity) of all the fossil horn cores suggested they belonged to adults or near-adults, I decided to concentrate on measurements of obviously adult specimens in the comparative collections. Because I could not always determine adulthood by examination of the cores themselves (frequently I could not remove the sheaths sufficiently), I relied on a dental state (upper and lower M3's both in at least Early Wear) as a rough index.

Appendix 1 presents the basic statistical parameters (\bar{x} = arithmetic mean, N = sample size, s = standard deviation) for each dental and horn-core category within *H. equinus*, *H. niger*, and each of the fossil samples. For *H. equinus* and *H. niger* the data are further broken down by sex, including a category in which known males, known females, and specimens of unknown sex are lumped. For *H. equinus*, *H. niger*, and those (few) fossil specimens for which matching left and right halves were available, only measurements on the left half were used to calculate the parameters in Appendix 1. All measurements were made in millimetres with the same dial-reading Helios calipers.

ANALYSIS OF THE MEASUREMENTS

Although a variety of statistical procedures, including multi-variate ones, could be used to analyse the numbers in Appendix 1, it was felt that the easily understood 't test' for statistically significant differences between two means, together with an intuitive appreciation for the size and patterning of differences, would be adequate to deal with the questions that prompted the analysis. Values

of 't' between paired means were calculated using a modified version of Programme BMDX70 on the CDC 6400 at the University of Washington computer centre (the same programme also calculated the means, standard deviations, and coefficients of variation found in Appendix 1). Those samples whose means were found to differ from one another at the 0.05 significance level or below are listed in Appendix 2. The sample with the larger mean is always to the left. In each case, the value of 't', the number of degrees of freedom (df), and the actual significance level of the differences (p) are given in succeeding columns.

Appendix 2, in conjunction with Appendix 1, can be used to support the following propositions:

(1) There is very little evidence for sexual dimorphism in tooth length in either *H. equinus* or *H. niger*. Such sex differences as may exist are small and there is reasonable justification for lumping measurements from both sexes in comparing *H. equinus* and *H. niger* with each other and with the fossil samples, which cannot be partitioned according to sex in any case. It is also relevant to point out that the coefficients of variation ($100s/\bar{x}$) (Appendix 1) are not substantially different for the mixed sex samples of teeth than for the single sex ones, suggesting again that lumping the sexes for comparison with the fossil samples is reasonable.

(2) The various teeth of *H. equinus* are longer than their counterparts in *H. niger*, the differences being especially great for the premolars. The premolars of *H. niger variati* are not significantly different in size from those of the remainder of the *H. niger* sample, but the molars are significantly longer, approaching those of *H. equinus* in length.

(3) The dental samples from Elands Bay, Elandsfontein, Bloembos, Swartklop, Eyre's Cave, Hawston, Lake Pleasant, and Klasies River Mouth are all very similar in mean measurements for any given category. Relatively few statistically significant differences can be demonstrated among these samples, and those that do exist tend to be small. Teeth in each of the cited samples are consistently shorter than corresponding teeth in *H. equinus*, the differences being especially marked for the molars. The premolars in the various samples tend to be significantly longer than those of *H. niger*, while the molars are roughly comparable in length to those of *H. niger*, though small differences in mean molar length between these samples and *H. niger* can be demonstrated statistically in some cases.

(4) Significant differences between the means of dental samples from Nelson Bay Cave, Oakhurst, and Uniondale on the one hand and those of the various fossil samples considered under (3) on the other are fairly common, with Nelson Bay, Oakhurst, and Uniondale means larger than the others in every case. Additionally, the means of the Nelson Bay, Oakhurst, and Uniondale dental samples differ from those discussed in (3) in being sometimes significantly larger and sometimes significantly smaller than those of *H. equinus*. At the same time, the means for both the molars and the premolars in the Nelson Bay, Oakhurst, and Uniondale samples tend to be significantly larger than those of *H. niger*.

Clearly there is justification for lumping Nelson Bay, Oakhurst, and Uniondale together as a group distinct from the other fossil samples. The peculiar behaviour of the Nelson Bay, Oakhurst, and Uniondale samples with respect of *H. equinus* strongly suggests that they are mixed, that is, that each contains material from more than one species, while the extent and nature of the mixture varies from dental category to dental category within each sample. Species mixture is particularly indicated for the Nelson Bay sample in which several dental categories exhibit relatively high coefficients of variation (Appendix 1), especially considering the comparatively small sample sizes.

The small dental samples from Melkhoutboom and Cradock Springs behave similarly to those from Nelson Bay, Oakhurst, and Uniondale with respect to the other samples, both fossil and comparative, except there is no instance in which a Melkhoutboom or Cradock Springs mean is significantly less than one for *H. equinus*.

(5) The *Hippotragus* skull in Glasgow that Broom assigned to *H. leucophaeus* is difficult to compare with the fossil samples because the only measurements available on it are maximum lengths of the entire premolar and molar rows. Intact molar and premolar rows are very poorly represented in the fossil samples. Additionally, alone among the measurements presented here, those on the Glasgow specimen were not made by the author, but were extracted from Mohr (1967: 62). Using these measurements, the Glasgow specimen is distinguishable from *H. equinus* by its significantly smaller upper and lower premolar rows and from *H. niger* by its significantly smaller upper premolar row. If the Glasgow skull derives from *H. leucophaeus*, this difference from *H. niger* is difficult to understand (a longer premolar row than in *H. niger* would be expected—see conclusions below based on proposition 3 above), and it is possible that a misprint in Mohr is responsible. (If the upper premolar row were 45,50 mm instead of 35,50 mm as given by Mohr, the Glasgow specimen would be indistinguishable from *H. niger* in upper premolar row length.) It must be concluded that the present study has not clarified the specific identity of the Glasgow skull, though on the basis of characters which are not considered here, but which may be seen in Mohr's photographs, I think it is highly likely the Glasgow specimen belongs to *H. niger*. This conclusion has been reached independently by Gentry (pers. comm.).

(6) Although the fossil horn cores cannot be 'sexed' to make them strictly comparable to those of *H. equinus* and *H. niger*, in both of which there is significant and substantial horn-core dimorphism, it is interesting that the average transverse diameter of the fossil specimens is closely comparable to that of both *H. equinus* and *H. niger* females, while their average longitudinal diameter significantly exceeds that of the females of either species. This suggests that the fossil males and females possessed smaller horn-core bases than the corresponding sexes in either *H. equinus* or *H. niger*, while the degree of transverse compression characterizing each sex in the fossil group was more comparable to that found in the sexes of *H. niger* than in those of *H. equinus*.

CONCLUSIONS

It seems reasonable to conclude that the relatively homogeneous material from Elands Bay, Elandsfontein, Bloembos, Swartklip, Eyre's Cave, Hawston, Lake Pleasant, and Klasies River Mouth derives from a single species of *Hippotragus* which may be differentiated from *H. equinus* by substantially smaller molars and premolars, and by smaller, more transversely compressed horn cores. It may be differentiated from *H. niger* by its larger premolars, higher premolar row to molar row length ratio and smaller horn cores. Since the various sites lie in or near the area where *H. leucophaeus* was encountered historically, and since there is nothing in the contrasts with *H. equinus* and *H. niger* that is contradicted by historical accounts of *H. leucophaeus*, it is only logical to assume that the species represented at the fossil sites is *Hippotragus leucophaeus*. The fact that a few small, but significant differences exist among the presumed *H. leucophaeus* samples is not surprising, considering their spread over a span of tens of thousands of years.

The most economical explanation of the relatively heterogeneous material from Oakhurst, Nelson Bay Cave, and Uniondale is that it results from a mixture of *H. leucophaeus* and a closely related, but significantly larger species. The most reasonable candidate for the second species is *H. equinus*, though if this is accepted, the data in Appendices 1 and 2 imply that the now extinct southern Cape *H. equinus* was significantly larger than the recent central African variety that dominates the comparative sample. The probable distributional overlap of *H. leucophaeus* and *H. equinus* at Uniondale, Oakhurst, and especially at Nelson Bay, where overlap seems to have lasted for several millennia, clearly suggests that the two forms are separate species and not simply subspecies. As indicated by Mohr (1967: 20–21), many nineteenth-century authors and some twentieth-century ones have regarded *H. leucophaeus* as only a subspecies of *H. equinus*. Interestingly, overlap in the vicinity of Nelson Bay Cave may have continued into historic times if, as Mohr (1967: 16) reasonably suggests, an animal seen and illustrated in 1778 by Gordon near Plettenberg Bay was a roan and not a blue antelope.

The small samples from Melkhoutboom and Cradock Springs are most reasonably assigned to *H. equinus*. Whether or not *H. leucophaeus* was also represented in the vicinity of these sites must remain uncertain until larger samples are collected.

The fossil data suggest that *H. leucophaeus* was both more widely distributed and more numerous in the past than at time of historic contact. In the earlier part of the Last Glacial, it occurred both east of Plettenberg Bay (at Klasies River Mouth) and west of the Hottentots Holland Mountains (at Swartklip and perhaps also at Elandsfontein).² During this time interval (roughly between 70 000 and 35 000 B.P.), *H. leucophaeus* may have been the only

² It is the geological antiquity and not the specific assignment of the material from Elandsfontein that is problematical.

species of *Hippotragus* in the southern Cape (at least south of the mountains of the Cape Folded Belt). Both well-dated, earlier Last Glacial sites have provided fairly large *Hippotragus* samples with no hint of species mixture. At both sites, the frequency of *H. leucophaeus* vs. that of other taxa in the fossil assemblages is relatively high, suggesting that *H. leucophaeus* was a fairly common antelope.

H. leucophaeus may have maintained its broader-than-historic distribution throughout the Last Glacial, though this cannot be established at present. It can be said, however, that it was fairly numerous near Nelson Bay Cave near the end of the Last Glacial, while in the early Holocene, it once again occurred far outside its historic limits, as far west as Elands Bay and as far east as Uniondale Shelter.

The time when the ranges of *H. equinus* and *H. leucophaeus* first overlapped remains uncertain, but some clues may be obtained by examination of dental samples from the different levels of Nelson Bay Cave. Although there is no statistical technique which will separate mixed Nelson Bay samples into discrete *H. equinus* and *H. leucophaeus* subsamples, it is possible to use an arbitrary cut-off point to determine if the extent of mixture seems to have changed through time. Molars are more useful than premolars in this context since they contrast more in mean size between *H. equinus* and *H. leucophaeus* (as found unmixed at Swartklip, Klasies River Mouth, etc.) than do premolars. Limited experimentation with the data in Appendix 1 showed that a useful arbitrary cut-off point was the mean length for each wear category of each *H. equinus* molar minus the standard deviation for that category. In Table 3, the number of molars smaller than this arbitrary standard in each of the major culture-stratigraphic units of Nelson Bay is presented in the left-hand column, the number of molars larger than the standard appears on the right. For the sake of comparison, the apparently homogeneous sample from Klasies River Mouth, considerably older than any of the Nelson Bay samples, has been partitioned in the same manner and included in the bottommost row of Table 3.

Table 3 clearly shows that the 11 000–8 000 year unit at Nelson Bay (Albany culture-stratigraphic unit) is characterized by a significantly larger number of teeth, longer than the arbitrary standard than are the other two Nelson Bay units or the Klasies unit. These data may be used to argue strongly that *H. equinus* only became prominent at Nelson Bay after 11 000 B.P. or even that it only first appeared there at that time. More sophisticated techniques applied to larger samples than are presently available may allow a more conclusive statement at some future date.

11 000 B.P. was a time when not only culture but also environment was changing at Nelson Bay Cave. Evidence from analysis of the entire fauna (Klein 1972b) indicates that extensive stretches of grassland present prior to 11 000 B.P. were shrinking, probably as a consequence of bush-forest encroachment, perhaps in combination with drowning of much of the coastal plain by the terminal Last Glacial rise in sea-level. It is entirely possible that this environmental change was what brought *H. equinus* into the area, or if it was already there, led

Table 3

Comparison of the frequencies of *Hippotragus* molars above and below an arbitrary standard length in the different culture-stratigraphic units of Nelson Bay and Klasies River Mouth caves.

Culture-stratigraphic units	Number of molars smaller than the <i>H. equinus</i> mean minus one standard deviation from the <i>H. equinus</i> mean	Number of molars larger than the <i>H. equinus</i> mean minus one standard deviation from the <i>H. equinus</i> mean	Approx. C-14 years B.P.
			5 000
Wilton (Nelson Bay)	5 (56%) A	4 (44%) B	
			8 000
Albany (Nelson Bay)	11 (20%) C	43 (80%) D	
			11 000
Robberg (Nelson Bay)	26 (74%) E	9 (26%) F	
			18 500
MAJOR TIME BREAK			
			≥ 30 000
Middle Stone Age (Klasies River Mouth)	105 (76%) G	34 (24%) H	
			780 000

Chi-square values

$$\frac{AB}{CD} = 5,027, p = 0,05-0,02$$

$$\frac{CD}{EF} = 25,413, p < 0,001$$

$$\frac{EF}{GH} = 0,024, p = 0,90-0,80$$

to its increase relative to *H. leucophaeus*, as suggested by Table 3. If so, we have evidence for a possible ecological contrast between *H. leucophaeus* and *H. equinus*—though both were probably mainly grazers, *H. leucophaeus* could be inferred to have preferred somewhat more open habitats than *H. equinus*. The same sort of contrast has been observed between *H. niger* and *H. equinus* (in this case it is *H. equinus* that seems to prefer the slightly more open situations—Child and Wilson 1964), though very little else is known about their ecological differences. It is interesting that the frequency of *H. leucophaeus* vs. *H. equinus* at Nelson Bay may have shifted again after c. 8 000 B.P. (as indicated by Table 3), since there is independent evidence for further environmental change around Nelson Bay at that time. Unfortunately, its precise nature remains undetermined (Klein 1972a).

At the time of historic contact, it seems probable that *H. leucophaeus* was already very much reduced in range and numbers from prior times and that Europeans and European weapons only delivered the *coup de grâce*. It is unclear what may have led to its decline prior to the arrival of Europeans, but the principal factor may have been habitat deterioration, following the introduction of domestic sheep. These have now been documented as early as A.D. 400 for the south-western Cape (Schweitzer & Scott 1973). Interestingly, *H. equinus* is presently in a state of decline which is not clearly linked to human predation (Ansell 1971: 46), but which may in fact relate in complex fashion to the introduction of domestic stock over much of its range. Future research at archaeological and palaeontological sites in the southern Cape should provide data to help explain the decline of *H. leucophaeus* as well as more information on its appearance, habitat preferences, and past distribution.

SUMMARY

The blue antelope, *Hippotragus leucophaeus*, was encountered by early European travellers to the Cape in a small area centring on the triangle Swellendam–Caledon–Bredasdorp. It was apparently never numerous in historic times and became extinct around A.D. 1800, before qualified scientists could make observations on live specimens. This paper analyses relevant fossil material from several Upper Pleistocene and Holocene localities in the southern Cape in an attempt to resolve some outstanding questions on the taxonomic status, distribution, and ecology of *H. leucophaeus*. It is concluded that it was a good species (not simply a subspecies of the roan, *H. equinus*), that at various times in the past it was both more numerous and more widely distributed than at time of historic contact, and that it probably preferred somewhat more open habitats than its close relative, *H. equinus*, with which it apparently overlapped throughout much of the Holocene, at least in the vicinity of Plettenberg Bay.

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M^1-M^3		<i>H. equinus</i>		<i>H. niger</i> subsp.		<i>H. niger variati</i>		Swartklip	Klasies	Nelson Bay
		Males	Females	Males	Females	Males	Females			
\bar{x}	72,52	70,35	70,77	66,63	64,64	71,60	—	67,37	63,10	69,00
N	15	23	66	31	30	1	—	3	2	1
s	3,316	2,670	2,985	3,454	3,475	—	—	3,157	—	—
V	4,6	3,8	4,2	5,2	5,4	—	—	4,7	—	—
<i>Elandsfontein</i>		<i>Glasgow</i>								
\bar{x}	69,50	66,50								
N	1	1								
s	—	—								
V	—	—								
P^2-P^4/M^1-M^3		<i>H. equinus</i>		<i>H. niger</i> subsp.		<i>H. niger variati</i>		Swartklip	Klasies	Glasgow
		Males	Females	Males	Females	Males	Females			
\bar{x}	0,740	0,745	0,748	0,697	0,708	0,647	—	0,761	0,808	0,549
N	10	22	54	24	24	1	—	1	2	1
s	0,044	0,034	0,035	0,030	0,029	—	—	—	0,009	—
V	5,9	4,6	4,7	4,3	4,1	—	—	—	1,1	—
Horn-core base—Medio-lateral (transverse) diameter		<i>H. equinus</i>		<i>H. niger</i> subsp.		<i>H. niger variati</i>				
		Male	Female	Male	Female	Male	Female			
		adults	all ages	adults	adults	adults	adults			
\bar{x}	49,05	38,35	42,93	49,42	39,64	60,15	MM,FF, all ages			
N	4	6	35	11	17	1	—			
s	5,608	3,038	6,631	5,150	3,854	—	—			
V	11,4	7,9	14,8	10,4	9,7	—	—			
<i>Nelson Bay</i>		<i>Elandsfontein</i>		<i>Sum of three previous</i>						
\bar{x}	42,60	43,14		42,21						
N	1	7		13						
s	—	3,405		3,537						
V	—	8,0		8,4						

Horn-core base—Antero-posterior (longitudinal) diameter

<i>H. equinus</i>				<i>H. niger</i> subsp.				<i>H. niger variati</i>		<i>Klastes</i>
Male		Female		Male		Female		Male	Female	
adults	MM,FF, all ages	adults	all ages	adults	all ages	adults	all ages	adults	all ages	
\bar{x} 59,38	44,40	50,64	55,97	48,11	55,97	—	—	82,85	—	51,54
N 4	6	35	37	17	37	—	—	1	—	5
s 8,960	4,317	9,142	12,638	4,772	12,638	—	—	—	—	5,482
V 15,1	9,7	18,1	22,6	12,9	22,6	—	—	—	—	10,6
<i>Nelson Bay</i>				<i>Sum of three previous</i>						
\bar{x} 54,20	53,47	52,78								
N 1	7	13								
s —	4,511	4,613								
V —	8,4	8,7								

Horn-core base—Medio-lateral diameter/antero-posterior diameter

<i>H. equinus</i>				<i>H. niger</i> subsp.				<i>H. niger variati</i>		<i>Klastes</i>
Male		Female		Male		Female		Male		
adults	MM,FF, all ages	adults	all ages	adults	all ages	adults	all ages	adults	all ages	
\bar{x}	0,830	0,865	0,853	0,729	0,825	0,726	0,788	—	0,726	0,794
N	4	6	35	11	17	1	37	—	1	5
s	0,034	0,025	0,039	0,040	0,036	—	0,063	—	—	0,042
V	4,1	2,8	4,5	5,5	4,4	—	8,0	—	—	5,3
<i>Nelson Bay</i>				<i>Sum of three previous</i>						
<i>Elandsfontein</i>										
\bar{x}	0,786		0,808		0,801					
N	1		7		13					
s	—		0,029		0,033					
V	—		3,6		4,1					

 dP₂

<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
NW		EW		NW		EW		NW		EW	
adults	all ages	adults	all ages	adults	all ages	adults	all ages	adults	all ages	adults	all ages
\bar{x} 12,50	13,00	12,23	13,10	12,20	13,03	12,20	13,03	13,38	12,12	12,95	12,30
N 1	7	6	1	2	4	2	4	4	13	13	1
s —	0,673	1,212	—	0,566	0,634	0,566	0,634	0,737	1,021	0,629	—
V —	5,2	9,9	—	4,6	4,8	4,6	4,8	5,5	3,4	4,9	—

<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	10,67	10,80	11,40	—	10,13	9,70	—	—	10,64	10,25	11,40
N	3	1	3	—	3	1	—	—	7	2	3
s	1,193	—	1,375	—	0,513	—	—	—	1,023	0,778	1,735
V	11,2	—	15,2	—	5,1	—	—	—	9,6	7,6	15,2
<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	10,54	10,10	—	10,60	13,50	—	9,20	11,10	12,62	11,60	11,50
N	5	2	—	6	2	—	1	1	5	3	1
s	0,744	1,414	—	0,853	3,818	—	—	—	1,891	0,208	—
V	7,1	14,0	—	8,0	28,3	—	—	—	15,0	1,8	—
<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	10,30	—	18,20	14,90	19,85	18,65	18,90	18,10	19,50	18,28
N	—	1	—	1	1	2	4	2	5	4	19
s	—	—	—	—	—	1,061	0,843	0,990	1,887	0,734	1,412
V	—	—	—	—	—	5,3	4,5	5,2	10,4	3,8	7,7
<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	15,50	15,46	—	15,50	—	15,40	—	16,10	15,50	15,44
N	—	1	5	—	2	—	2	—	3	1	7
s	—	—	1,414	—	1,061	—	0,849	—	1,212	—	0,996
V	—	—	7,4	—	6,8	—	5,5	—	7,5	—	6,5

Swartklip				Klasies				Nelson Bay			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 17,27	—	16,20	—	17,44	19,15	—	16,53	18,50	18,20	17,90	17,95
N 6	—	2	—	8	2	—	4	7	3	3	2
S 0,943	—	0,566	—	0,573	0,919	—	0,427	0,872	0,954	0,854	0,495
V 5,5	—	3,5	—	3,3	4,8	—	2,6	4,7	5,2	4,8	2,8

Lake Pleasant			
NW	EW	MW	LW
\bar{x} —	—	17,00	—
N —	—	1	—
S —	—	—	—
V —	—	—	—

dP₄

<i>H. equinus</i> —Males			
NW	EW	MW	LW
\bar{x} —	—	27,10	24,57
N —	—	3	12
S —	—	1,825	1,244
V —	—	6,7	5,1

H. equinus—Females

NW	EW	MW	LW
—	31,00	28,28	26,33
—	1	4	3
—	—	2,090	0,551
—	—	7,4	2,1

H. equinus—MM,FF,??

NW	EW	MW	LW
29,30	31,00	27,73	25,15
1	1	10	21
—	—	1,926	1,529
—	—	6,9	6,1

H. niger subsp.—Males

NW	EW	MW	LW
—	—	24,50	22,78
—	—	1	6
—	—	—	1,339
—	—	—	5,9

H. niger subsp.—Females

NW	EW	MW	LW
—	—	24,65	23,10
—	—	2	2
—	—	—	1,556
—	—	—	6,7

H. niger subsp.—MM,FF,??

NW	EW	MW	LW
—	—	24,95	22,86
—	—	4	8
—	—	0,704	1,284
—	—	2,8	5,6

Swartklip				Klasies				Nelson Bay			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 27,57	28,70	26,50	—	27,95	27,64	29,60	23,18	28,28	31,70	29,05	24,05
N 6	1	2	—	6	5	1	4	5	1	2	4
S 1,518	—	2,121	—	0,703	1,610	—	0,903	1,130	—	0,778	1,134
V 5,5	—	8,0	—	2,5	5,8	—	3,9	4,0	—	2,7	4,6

				<i>Lake Pleasant</i>			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	25,20	—
	N	—	—	—	—	1	—
	s	—	—	—	—	—	—
	V	—	—	—	—	—	—
				<i>Elandsfontein</i>			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	25,40	—
	N	—	—	—	—	2	—
	s	—	—	—	—	1,414	—
	V	—	—	—	—	5,6	—
				<i>H. equinus</i> —Males			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	18,10	—
	N	—	—	—	—	3	—
	s	—	—	—	—	0,700	—
	V	—	—	—	—	3,9	—
				<i>H. niger</i> subsp.—Males			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	15,20	—
	N	—	—	—	—	1	—
	s	—	—	—	—	—	—
	V	—	—	—	—	—	—
				<i>Swartklip</i>			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	16,63	—
	N	—	—	—	—	3	—
	s	—	—	—	—	0,379	—
	V	—	—	—	—	2,3	—
				<i>Klasies</i>			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	15,80	—
	N	—	—	—	—	3	—
	s	—	—	—	—	0,656	—
	V	—	—	—	—	4,2	—
				<i>H. equinus</i> —Females			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	18,43	—
	N	—	—	—	—	3	—
	s	—	—	—	—	0,404	—
	V	—	—	—	—	2,2	—
				<i>H. niger</i> subsp.—Females			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	15,05	—
	N	—	—	—	—	2	—
	s	—	—	—	—	1,343	—
	V	—	—	—	—	8,9	—
				<i>Nelson Bay</i>			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	15,53	—
	N	—	—	—	—	3	—
	s	—	—	—	—	1,266	—
	V	—	—	—	—	8,2	—
				<i>H. equinus</i> —MM,FF,??			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	17,25	—
	N	—	—	—	—	4	—
	s	—	—	—	—	1,187	—
	V	—	—	—	—	6,7	—
				<i>H. niger</i> subsp.—MM,FF,??			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	15,20	—
	N	—	—	—	—	1	—
	s	—	—	—	—	—	—
	V	—	—	—	—	—	—
				<i>H. equinus</i> —MM,FF,??			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	17,81	—
	N	—	—	—	—	8	—
	s	—	—	—	—	1,038	—
	V	—	—	—	—	5,8	—
				<i>H. equinus</i> —MM,FF,??			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	21,67	—
	N	—	—	—	—	3	—
	s	—	—	—	—	0,723	—
	V	—	—	—	—	3,4	—
				<i>H. equinus</i> —MM,FF,??			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	21,80	—
	N	—	—	—	—	1	—
	s	—	—	—	—	—	—
	V	—	—	—	—	—	—
				<i>H. equinus</i> —Females			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	20,53	—
	N	—	—	—	—	3	—
	s	—	—	—	—	1,102	—
	V	—	—	—	—	5,4	—
				<i>H. equinus</i> —Males			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	22,25	—
	N	—	—	—	—	2	—
	s	—	—	—	—	—	—
	V	—	—	—	—	—	—
				<i>H. equinus</i> —Males			
				NW	EW	MW	LW
dP ³	\bar{x}	NW	EW	—	—	20,33	—
	N	—	—	—	—	12	—
	s	—	—	—	—	0,963	—
	V	—	—	—	—	4,7	—

<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	18,00	—	—	18,67	—
N	—	—	—	2	—	—	3	—
S	—	—	—	0,707	—	—	1,258	—
V	—	—	—	3,9	—	—	6,7	—
								18,35
								8
								1,110
								6,0
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	20,07	—	—	—	—
N	—	—	—	3	—	—	—	—
S	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—
								20,00
								1
								—
								—
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	18,60	—	—	—	—
N	—	—	—	1	—	—	—	—
S	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—
								21,15
								2
								0,212
								1,0
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	18,70	—	—	—	—
N	—	—	—	1	—	—	—	—
S	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—
								19,10
								1
								—
								—
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	22,40	—	—	—	—
N	—	—	—	1	—	—	—	—
S	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—
								22,15
								2
								0,636
								2,9
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	20,46	—	—	—	—
N	—	—	—	10	—	—	—	—
S	—	—	—	0,735	—	—	—	—
V	—	—	—	3,6	—	—	—	—
								21,63
								11
								25
								1,201
								5,3
<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM, FF, ??		
NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	—	17,70	—	—	—	—
N	—	—	—	1	—	—	—	—
S	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—
								19,33
								3
								10
								1,415
								7,3
								8,3

dP⁴

				<i>Nelson Bay</i>			
				EW	MW	LW	
	NW						
\bar{x}	—			22,67	—	—	
N	—			3	—	—	
s	—			1,501	—	—	
V	—			6,6	—	—	
				<i>Klasies</i>			
				EW	MW	LW	
	NW						
\bar{x}	19,15			19,95	18,50	—	
N	2			2	1	—	
s	—			0,212	—	—	
V	—			1,1	—	—	
				<i>Uniondale</i>			
				EW	MW	LW	
	NW						
\bar{x}	—			—	—	17,70	
N	—			—	—	1	
s	—			—	—	—	
V	—			—	—	—	
				<i>Eyre's Cave</i>			
				EW	MW	LW	
	NW						
\bar{x}	20,00			—	—	—	
N	1			—	—	—	
s	—			—	—	—	
V	—			—	—	—	
				<i>H. equinus—Males</i>			
				EW	MW	LW	
	NW						
\bar{x}	13,40			14,28	13,90	—	
N	2			6	1	—	
s	—			0,988	—	—	
V	—			6,8	—	7,2	
				<i>H. niger subsp.—Males</i>			
				EW	MW	LW	
	NW						
\bar{x}	13,26			11,77	11,37	—	
N	7			13	3	—	
s	1,519			1,387	1,050	—	
V	11,5			11,8	9,2	—	
				<i>H. niger variati—Males</i>			
				EW	MW	LW	
	NW						
\bar{x}	—			12,60	—	—	
N	—			1	—	—	
s	—			—	—	—	
V	—			—	—	—	
				<i>H. equinus—Females</i>			
				EW	MW	LW	
	NW						
\bar{x}	12,65			12,80	10,80	—	
N	4			4	1	—	
s	0,914			0,497	—	—	
V	3,9			—	—	—	
				<i>H. niger subsp.—Females</i>			
				EW	MW	LW	
	NW						
\bar{x}	12,18			12,15	11,90	10,10	
N	5			15	4	1	
s	0,646			1,006	0,627	—	
V	5,3			8,3	5,3	—	
				<i>H. niger subsp.—MM,FF,??</i>			
				EW	MW	LW	
	NW						
\bar{x}	12,81			11,96	11,67	10,10	
N	12			32	7	1	
s	1,310			1,125	0,804	—	
V	10,2			9,4	6,9	—	
				<i>Klasies</i>			
				EW	MW	LW	
	NW						
\bar{x}	12,45			11,80	13,48	14,20	
N	2			3	5	1	
s	0,636			0,458	1,472	—	
V	5,1			3,9	10,9	—	

<i>Nelson Bay</i>				<i>Bloembos</i>				<i>Hawston</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 13,33	13,28	—	13,00	—	13,15	—	—	—	—	13,10	—
N 6	10	—	1	—	1	—	—	—	—	1	—
s 0,905	1,589	—	—	—	—	—	—	—	—	—	—
V 6,8	12,0	—	—	—	—	—	—	—	—	—	—
<i>Oakhurst</i>				<i>H. equinus—Males</i>				<i>H. equinus—Females</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 12,65	—	—	—	—	18,30	16,80	16,77	—	18,46	17,47	17,25
N 2	—	—	—	—	10	1	3	—	25	7	6
s 12,02	—	—	—	—	0,793	—	0,702	—	0,924	0,883	0,871
V 9,5	—	—	—	—	4,3	—	4,1	—	5,0	5,1	5,1
<i>P₃</i>				<i>H. equinus—Males</i>				<i>H. equinus—MM,FF,??</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 15,30	18,15	17,37	18,70	—	18,30	16,80	16,77	15,30	18,46	17,47	17,25
N 1	8	3	1	—	10	1	3	1	25	7	6
s —	0,832	1,097	—	—	0,793	—	0,702	—	0,924	0,883	0,871
V —	4,6	6,3	—	—	4,3	—	4,1	—	5,0	5,1	5,1
<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM,FF,??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} —	15,84	15,57	14,00	14,50	15,89	15,22	14,60	14,50	15,80	15,82	14,40
N —	14	9	2	1	16	6	4	1	32	18	6
s —	1,136	1,084	0,707	—	0,804	1,080	1,257	—	0,943	2,470	1,070
V —	5,7	7,0	5,1	—	5,3	7,1	8,6	—	5,9	15,6	7,4
<i>H. niger</i> variant — Males				<i>Swartklip</i>				<i>Klasies</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} —	17,05	—	—	—	16,98	17,30	—	17,20	16,73	16,76	16,00
N —	1	—	—	—	4	1	—	3	4	5	2
s —	—	—	—	—	0,613	—	—	1,179	0,727	0,716	1,131
V —	—	—	—	—	3,6	—	—	6,9	4,3	4,3	7,1

<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Bloembos</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	17,50	18,23	19,70	—	17,20	17,15	—	—	—	17,60	—
N	18	4	1	—	2	2	—	—	—	1	—
S	1,445	0,709	—	—	—	0,636	—	—	—	—	—
V	8,3	3,9	—	—	—	3,7	—	—	—	—	—
<i>Hawston</i>				<i>Oakhurst</i>				<i>Untondale</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	15,55	—	16,60	—	—	—	—	—	—	18,40
N	—	1	—	1	—	—	—	—	—	—	1
S	—	—	—	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—	—	—	—
<i>Melkhouboom</i>											
NW	EW	MW	LW								
\bar{x}	—	—	17,60								
N	—	—	1								
S	—	—	—								
V	—	—	—								
<i>P₄</i>				<i>H. equinus</i> —Males				<i>H. equinus</i> —MM,FF,??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	18,38	17,97	19,50	—	18,80	18,70	18,18	—	18,51	18,34	18,74
N	6	3	1	—	9	1	4	—	25	5	9
S	1,251	0,551	—	—	0,487	—	0,896	—	0,932	0,658	0,934
V	6,8	3,1	—	—	2,6	—	4,9	—	5,0	3,6	5,0
<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM,FF,??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	15,78	15,61	14,70	15,40	16,00	16,14	15,58	15,30	15,94	15,74	15,38
N	13	8	1	1	16	5	5	3	31	16	8
S	0,878	1,067	—	—	1,099	0,789	1,027	0,500	0,981	0,915	1,102
V	5,6	6,8	—	—	6,9	4,9	6,6	3,3	6,2	5,8	7,2

<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females				<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	16,85	—	—	18,43	18,80	—	—	18,43	18,80	—	—	18,43	18,80	—
N	—	1	—	—	3	2	—	—	3	2	—	—	3	2	—
S	—	—	—	—	0,838	0,283	—	—	0,838	0,283	—	—	0,838	0,283	—
V	—	—	—	—	4,5	1,5	—	—	4,5	1,5	—	—	4,5	1,5	—
<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Eyre's Cave</i>				<i>Swartklip</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	19,20	17,70	16,10	—	17,60	18,60	17,00	—	17,60	18,60	17,00	—	17,52	16,65	16,15
N	2	1	1	—	1	1	1	—	1	1	1	—	5	2	2
S	1,414	—	—	—	—	—	—	—	—	—	—	—	0,421	—	0,212
V	7,4	—	—	—	—	—	—	—	—	—	—	—	2,4	—	1,3
<i>Hawston</i>				<i>Swartklip</i>				<i>Eyre's Cave</i>				<i>Swartklip</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	16,80	—	—	—	16,60	—	—	—	16,60	—	—	—	17,75	—
N	—	1	—	—	—	1	—	—	—	1	—	—	—	1	—
S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females				<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	23,70	22,76	17,20	—	23,23	23,27	20,14	—	23,23	23,27	20,14	—	23,55	23,00	19,26
N	7	18	1	—	3	12	5	—	3	12	5	—	11	45	10
S	1,362	1,537	—	—	1,903	1,379	0,594	—	1,903	1,379	0,594	—	1,355	1,399	1,385
V	6,5	6,8	—	—	8,2	5,9	2,9	—	8,2	5,9	2,9	—	5,8	6,1	7,2
<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females				<i>H. niger varians</i> —Males				<i>H. niger varians</i> —Females			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	20,95	20,13	17,93	—	20,90	20,14	16,55	—	20,90	20,14	16,55	—	21,35	20,12	17,20
N	2	23	8	—	1	22	8	—	1	22	8	—	4	48	18
S	1,626	1,238	1,881	—	—	1,132	1,478	—	—	1,132	1,478	—	1,256	1,157	1,719
V	7,8	6,1	10,5	—	—	5,6	8,9	—	—	5,6	8,9	—	5,9	5,8	10,0

M₁

<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	23,77	22,01	19,30	—	22,91	21,51	19,83	—	23,32	21,74	19,72
N	9	23	1	—	10	16	4	—	19	44	5
S	1,629	1,111	—	—	1,426	1,240	0,846	—	1,545	1,263	0,769
V	6,9	5,0	—	—	6,2	5,8	4,3	—	6,6	5,8	3,9
<i>H. niger</i> variati — Males				<i>Swartklip</i>				<i>Klasies</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	23,95	—	—	—	21,64	—	22,33	22,96	22,75	20,00
N	—	1	—	—	—	5	—	4	7	13	1
S	—	—	—	—	—	—	—	1,678	1,414	2,788	—
V	—	—	—	—	—	—	—	7,5	6,2	10,1	—
<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Bloembos</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	24,85	25,12	22,98	24,45	22,30	21,05	—	—	—	22,55	—
N	2	5	8	2	2	4	—	—	—	1	—
S	4,031	3,091	1,651	1,202	0,707	0,493	—	—	—	—	—
V	16,2	12,3	7,2	4,9	3,2	2,3	—	—	—	—	—
<i>Hawston</i>				<i>Eyre's Cave</i>				<i>Oakhurst</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	20,00	21,80	—	19,80	—	—	29,50	22,90	—
N	—	—	1	1	—	1	—	—	1	1	—
S	—	—	—	—	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—	—	—	—	—
<i>Melkhouboom</i>											
NW	EW	MW	LW								
\bar{x}	—	25,85	—								
N	—	1	—								
S	—	—	—								
V	—	—	—								

M ₃	<i>H. equinus</i> —Males			<i>H. equinus</i> —Females			<i>H. equinus</i> —MM,FF,??		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	30,20	30,29	31,32	—	30,23	31,90	29,56	30,22	31,47
N	1	8	5	—	6	5	3	21	15
s	—	1,664	1,985	—	2,153	1,357	0,602	1,709	1,479
V	—	5,5	6,3	—	7,1	4,3	2,0	5,7	4,7
	<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM,FF,??		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	28,90	27,67	29,43	27,40	28,02	28,97	28,15	27,84	29,14
N	1	16	10	1	16	9	2	33	23
s	—	2,856	1,975	—	1,294	1,796	1,061	2,154	1,811
V	—	10,3	6,7	—	4,6	6,0	3,8	7,7	6,2
	<i>H. niger variati</i> —Males			<i>Swartklip</i>			<i>Klasies</i>		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	32,50	—	—	28,48	26,60	24,00	28,31
N	—	—	1	—	—	5	2	4	6
s	—	—	—	—	—	0,626	0,141	2,211	1,376
V	—	—	—	—	—	2,2	0,5	9,2	4,7
	<i>Nelson Bay</i>			<i>Elandsfontein</i>			<i>Bloembos</i>		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	31,50	29,96	30,34	28,40	27,75	28,10	—	—	29,55
N	1	5	11	1	2	4	—	—	1
s	—	2,079	3,088	—	1,768	0,627	—	—	—
V	—	6,9	10,2	—	6,4	2,2	—	—	—
	<i>Eyre's Cave</i>								
	NW	EW	MW						
\bar{x}	—	—	27,90						
N	—	—	1						
s	—	—	—						
V	—	—	—						

P²

<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
—	16,47	17,70	17,60	—	16,87	17,38	17,82	—	16,94	17,12	17,94
—	7	3	1	—	13	4	4	—	32	13	10
N	—	—	—	—	0,998	1,670	1,597	—	1,004	1,141	1,852
S	1,188	0,500	—	—	5,9	9,6	9,0	—	7,0	6,7	10,3
V	7,2	2,8	—	—	—	—	—	—	—	—	—
<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM, FF, ??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
—	15,45	14,93	14,55	13,90	15,36	15,55	14,63	13,90	15,43	14,84	14,37
—	13	8	2	1	15	4	6	1	31	16	9
N	—	—	—	—	1,351	0,480	1,232	—	1,179	0,974	1,235
S	1,144	0,819	0,495	—	8,8	3,1	8,4	—	7,6	6,6	8,6
V	7,4	5,5	3,4	—	—	—	—	—	—	—	—
<i>H. niger varianti</i> —Males				<i>Swartklip</i>				<i>Klasies</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
—	—	14,80	—	—	—	17,05	—	17,00	16,70	—	17,67
—	—	1	—	—	—	2	—	1	3	—	3
N	—	—	—	—	—	—	—	—	1,852	—	1,301
S	—	—	—	—	—	—	—	—	11,1	—	7,4
V	—	—	—	—	—	—	—	—	—	—	—
<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Hawston</i>			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
—	17,19	18,30	16,13	—	16,30	—	16,90	—	—	—	16,10
—	8	3	3	—	1	—	1	—	—	—	1
N	—	—	—	—	—	—	—	—	—	—	—
S	1,410	1,114	0,802	—	—	—	—	—	—	—	—
V	8,2	6,1	5,0	—	—	—	—	—	—	—	—
<i>Eyre's Cave</i>											
NW	EW	MW	LW								
—	—	—	18,20								
—	—	—	1								
N	—	—	—								
S	—	—	—								
V	—	—	—								

P ³	<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	16,65	16,76	17,00	17,30	—	17,38	17,95	17,52	16,50	17,12	17,30	17,69
N	2	7	3	1	—	13	4	6	3	33	12	10
s	0,495	0,263	0,557	—	—	0,896	1,047	1,074	0,436	0,781	1,470	0,968
V	3,0	1,6	3,3	—	—	5,2	5,8	6,1	2,6	4,6	8,5	5,5
	<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	14,50	15,34	15,28	15,70	14,00	15,18	15,00	14,29	14,38	15,28	15,08	14,39
N	3	14	10	1	1	14	5	7	4	31	19	9
s	0,794	1,029	0,882	—	—	0,584	0,731	0,878	0,695	0,798	0,769	0,920
V	5,5	6,7	5,8	—	—	3,9	4,9	6,1	4,8	5,2	5,1	6,4
	<i>H. niger</i> varianti—Males				<i>Swartklip</i>				<i>Klasies</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	15,70	—	—	—	17,80	17,70	15,70	16,68	16,65	15,40
N	—	—	1	—	—	—	1	1	1	5	2	2
s	—	—	—	—	—	—	—	—	—	1,392	—	0,849
V	—	—	—	—	—	—	—	—	—	8,3	—	5,5
	<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Hawston</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	16,70	17,30	19,00	17,23	—	16,90	—	17,20	—	—	—	15,90
N	1	4	1	4	—	1	—	1	—	—	—	1
s	—	1,892	—	0,750	—	—	—	—	—	—	—	—
V	—	11,0	—	4,4	—	—	—	—	—	—	—	—
	<i>Eyre's Cave</i>				<i>Uniondale</i>							
	NW	EW	MW	LW	NW	EW	MW	LW				
\bar{x}	—	—	—	17,40	—	—	—	16,70				
N	—	—	—	1	—	—	—	1				
s	—	—	—	—	—	—	—	—				
V	—	—	—	—	—	—	—	—				

P ⁴	<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	15,95	17,33	16,00	—	16,06	16,83	15,85	16,30	16,28	16,98	15,71
N	—	6	4	1	—	13	3	6	1	33	10	12
s	—	0,414	0,900	—	—	1,121	0,153	1,082	—	0,898	0,671	1,093
V	—	2,6	5,2	—	—	7,0	0,9	6,8	—	5,5	4,0	7,0
	<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	14,87	14,66	14,03	14,05	14,48	14,22	12,80	14,05	14,72	14,46	13,22
N	—	13	9	3	2	14	5	6	2	30	16	11
s	—	0,814	0,949	1,343	0,212	0,831	0,870	1,145	0,212	0,822	0,863	1,186
V	—	5,5	6,5	9,6	1,5	5,7	6,1	8,9	1,5	5,6	6,0	9,0
	<i>H. niger varianti</i> —Males				<i>Swarthklip</i>				<i>Klasies</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	14,65	—	—	15,25	—	16,10	14,50	14,26	14,40	15,37
N	—	—	1	—	—	2	—	2	1	10	2	3
s	—	—	—	—	—	1,344	—	2,121	—	1,034	2,546	1,102
V	—	—	—	—	—	8,8	—	13,2	—	7,3	17,7	7,2
	<i>Nelson Bay</i>				<i>Elands Bay</i>				<i>Uniondale</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	16,80	15,38	13,50	17,50	—	15,00	15,40	—	—	—	—	18,40
N	1	11	1	2	—	1	1	—	—	—	—	1
s	—	1,195	—	—	—	—	—	—	—	—	—	—
V	—	7,8	—	—	—	—	—	—	—	—	—	—
	<i>Eyre's Cave</i>											
	NW	EW	MW	LW								
\bar{x}	—	—	—	13,80								
N	—	—	—	1								
s	—	—	—	—								
V	—	—	—	—								

M ²	<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	25,67	26,11	25,91	23,40	25,27	25,24	25,39	23,96	24,99	25,66	25,38	23,69
N	3	8	11	1	3	5	18	5	11	18	52	8
s	1,155	1,127	1,069	—	0,306	2,026	1,630	0,577	0,817	1,385	1,579	0,611
V	4,5	4,3	4,1	—	1,2	8,0	6,4	2,4	3,3	5,4	6,2	2,6
<i>H. niger</i> subsp. — Males												
	<i>H. niger</i> subsp. — Males				<i>H. niger</i> subsp. — Females				<i>H. niger</i> subsp. — MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	24,73	23,72	—	—	24,33	23,07	21,30	—	24,61	23,31	21,30
N	—	9	24	—	—	4	22	5	—	13	55	5
s	—	0,782	1,489	—	—	1,646	1,508	1,017	—	1,060	1,501	1,017
V	—	3,1	6,3	—	—	6,8	6,5	4,8	—	4,3	6,4	4,8
<i>H. niger varians</i> —Males												
	<i>H. niger varians</i> —Males				<i>Swartklip</i>				<i>Klasies</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	26,00	—	—	25,30	21,70	—	22,18	22,65	21,85	23,50
N	—	—	1	—	—	1	2	—	5	2	11	1
s	—	—	—	—	—	—	0,566	—	0,789	0,495	0,588	—
V	—	—	—	—	—	—	2,6	—	3,6	2,2	2,7	—
<i>Nelson Bay</i>												
	<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Melkhouboom</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	24,50	22,83	—	24,50	22,55	22,85	23,00	—	—	24,90	—	24,60
N	2	7	—	1	2	2	1	—	—	1	—	1
s	2,828	1,285	—	—	0,353	0,919	—	—	—	—	—	—
V	11,5	5,6	—	—	1,6	4,0	—	—	—	—	—	—
<i>Cradock Springs</i>												
	<i>Cradock Springs</i>											
	NW	EW	MW	LW								
\bar{x}	28,00	27,10	—	—								
N	1	1	—	—								
s	—	—	—	—								
V	—	—	—	—								

M ³	<i>H. equinus</i> —Males			<i>H. equinus</i> —Females			<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	NW	EW	MW	NW	EW	MW	LW
\bar{x}	24,00	22,71	25,07	—	22,20	24,89	23,17	22,78	24,76	25,58
N	3	7	6	—	4	15	6	21	34	6
s	0,917	1,216	1,442	—	0,572	1,036	1,462	1,101	1,061	1,065
V	3,8	5,4	5,8	—	2,6	4,2	6,3	4,9	4,4	4,2
	<i>H. niger</i> subsp.—Males			<i>H. niger</i> subsp.—Females			<i>H. niger</i> subsp.—MM,FF,??			
	NW	EW	MW	NW	EW	MW	NW	EW	MW	LW
\bar{x}	23,03	22,70	23,59	22,40	22,19	23,65	22,78	22,47	23,57	24,36
N	3	10	18	2	13	11	5	26	34	5
s	0,503	0,794	1,182	0,990	1,592	1,258	0,701	1,303	1,143	1,946
V	2,2	4,2	5,0	4,4	7,2	5,3	3,1	5,8	4,9	8,0
	<i>H. niger variati</i> —Males			<i>Swartklip</i>			<i>Klasies</i>			
	NW	EW	MW	NW	EW	MW	NW	EW	MW	LW
\bar{x}	—	—	27,60	23,00	21,00	22,30	18,88	20,74	21,94	23,18
N	—	—	1	1	1	1	4	9	7	4
s	—	—	—	—	—	—	0,275	1,495	0,787	1,422
V	—	—	—	—	—	—	1,5	7,2	3,6	6,1
	<i>Nelson Bay</i>			<i>Elandsfontein</i>			<i>Eyre's Cave</i>			
	NW	EW	MW	NW	EW	MW	NW	EW	MW	LW
\bar{x}	24,75	21,28	24,62	—	21,50	22,75	—	—	—	24,10
N	2	6	5	—	1	2	—	—	—	1
s	0,495	1,462	0,739	—	—	1,485	—	—	—	—
V	2,0	6,9	3,0	—	—	6,5	—	—	—	—

Appendix 2

List of samples for which statistically significant mean differences exist, by category. t = value of 'Student's t ', df = degrees of freedom, p = significance level. He = *H. equinus*, Hnv = *H. niger*, ZW = Swartklip, KRM = Klasies River Mouth, NBC = Nelson Bay Cave, EFT = Elandsfontein, BMB = Bloemboos, HTN = Hawston, EC = Eyre's Cave, LP = Lake Pleasant, UND = Uniondale, OAK = Oakhurst, MHB = Melkhoutboom, CS = Cradock Springs, GGW = Glasgow, MM = Males, FF = Females.

	t	df	p	P_2-P_4	t	df	p
dP_2-dP_4				M_1-M_3			
He > Hn	6,55	40	< 0,001	ZW > Hn	3,83	52	< 0,001
ZW > Hn	4,43	15	< 0,001	BMB > Hn	3,32	51	0,002
KRM > Hn	2,42	13	0,031	BMB > Hnv	13,46	2	0,005
dP_2-dP_4				P_2-P_4			
He > KRM	2,19	40	0,034	He > Hn	13,82	109	< 0,001
He > Hn	5,66	50	< 0,001	He > Hnv	3,31	55	0,002
P_2-P_4				He > GGW	6,39	54	< 0,001
He > Hn	12,48	81	< 0,001	Hn > GGW	4,09	54	< 0,001
He > Hnv	3,29	31	0,002	KRM > Hn	2,62	57	0,011
He > KRM	3,01	30	0,005	M^1-M^3			
He > GGW	2,33	30	0,05-0,02	He > Hn	9,30	132	< 0,001
ZW > Hn	3,43	53	0,001	He > KRM	3,61	66	0,001
NBC > Hn	3,67	51	0,001	HnMM > HnFF	2,25	59	0,028
BMB > Hn	3,52	52	0,001	Hnv > Hn	2,45	68	0,017
BMB > Hnv	3,43	53	0,021	P_2-P_4			
M_1-M_3				M^1-M^3			
He > Hn	11,22	106	< 0,001	He > Hn	7,69	106	< 0,001
He > ZW	4,58	47	< 0,001	He > Hnv	4,02	54	< 0,001
He > EC	4,23	44	< 0,001	He > GGW	5,63	53	< 0,001
He > EFT	4,49	46	< 0,001	Hn > GGW	4,99	53	< 0,001
He > BMB	2,54	45	0,014	Hn > Hnv	2,48	54	0,015
Hnv > Hn	2,36	63	0,021	ZW > Hn	2,06	53	0,044
Hnv > ZW	5,07	4	0,007	KRM > He	2,42	54	0,019
Hnv > EFT	4,35	3	0,022	KRM > Hn	5,13	54	< 0,001
ZW > EC	4,10	3	0,026	KRM > GGW	23,50	1	0,05-0,02
P_2-P_4				KRM > Hnv	13,53	2	0,005
M_1-M_3				HORN-CORE BASES			
He > Hn	4,28	80	< 0,001	Medio-lateral diameter (all ages for He and Hn)			
He > Hnv	2,20	31	0,035				

HeMM > HeFF	t	df	p
HnMM > HnFF	3,85	14	0,001
Hnv > He	5,06	30	< 0,001
	3,77	35	0,001
Antero-posterior diameter (all ages for He and Hn)			
HeMM > HeFF	t	df	p
HnMM > HnFF	3,54	19	0,002
Hn > He	6,10	30	< 0,001
Hnv > Hn	2,04	70	0,045
Hnv > He	3,34	37	0,002
	4,92	35	< 0,001
Medio-lateral diameter/antero-posterior diameter (all ages for He and Hn)			
HnFF > HnMM	t	df	p
He > Hn	4,86	30	< 0,001
Hnv > Hn	5,28	70	< 0,001
He > KRM	2,97	37	0,005
He > EFT	3,18	38	0,003
	2,93	40	0,006
Medio-lateral diameter (M_3 in occlusion for He, Hn, and Hnv)			
HeMM > HnFF	t	df	p
HeMM > HeFF	4,05	19	0,001
HeMM > KRM	3,96	8	0,004
HeMM > KRM + NBC + EFT	2,59	7	0,036
HnMM > HnFF	2,96	15	0,013
HnMM > HeFF	5,75	26	< 0,001
HnMM > HnFF	4,79	15	< 0,001
HnMM > KRM	3,29	14	0,005
HnMM > KRM + NBC + EFT	4,05	22	< 0,001
Hnv > KRM	6,39	5	0,001
Hnv > EFT	6,52	7	< 0,001
EFT > HnFF	2,08	22	0,049
EFT > HeFF	2,64	11	0,023
KRM + NBC + EFT > HeFF	2,30	17	0,034
Antero-posterior diameter (M_3 in occlusion for He, Hn, and Hnv)			
HeMM > HeFF	t	df	p
HeMM > HnFF	3,59	8	0,007
HnMM > HnFF	3,59	19	0,002
HnMM > HnFF	7,83	26	< 0,001
HnMM > HeFF	6,17	15	< 0,001
HnMM > KRM	3,86	14	0,002
HnMM > EFT	4,06	16	0,001
HnMM > KRM + NBC + EFT	5,49	22	< 0,001
KRM > HeFF	2,42	9	0,039
EFT > HeFF	3,69	11	0,004
EFT > HnFF	2,54	22	0,019
KRM + EFT + NBC > HeFF	3,75	17	0,002
KRM + EFT + NBC > HnFF	2,70	28	0,012
Medio-lateral diameter/anterior-posterior diameter (M_3 in occlusion for He, Hn, and Hnv)			
HeMM > HnMM	t	df	p
HeFF > HnMM	4,44	13	0,001
HeFF > KRM	7,49	15	< 0,001
HeFF > EFT	3,54	9	0,006
HeFF > EFT + KRM + NBC	3,82	11	0,003
HeFF > HnFF	4,29	17	< 0,001
HeFF > NBC	2,50	21	0,021
KRM > HnMM	2,98	5	0,031
EFT > HnMM	2,94	14	0,011
KRM + EFT + NBC > HnMM	4,47	16	< 0,001
EFT > Hnv	4,81	22	< 0,001
HnFF > HnMM	3,60	7	0,009
	6,53	26	< 0,001
Medio-lateral diameter/anterior-posterior diameter (M_3 in occlusion for He, Hn, and Hnv)			
dP ₂ NW	t	df	p
He > ZW	5,71	7	0,001
He > KRM	5,30	8	0,001
dP ₂ EW			
He > Hn	6,30	18	< 0,001
He > ZW	5,21	13	< 0,001
NBC > Hn	2,35	10	0,040

	t	df	p		t	df	p
dP ₂ MW	2,46	13	0,029	dP ₄ NW	6,67	2	0,022
He > Hn	5,55	2	0,031	He > KRM	2,72	12	0,019
NBC > LP	2,89	8	0,020	dP ₄ MW	2,36	10	0,040
dP ₃ NW	2,83	13	0,014	He > Hn	5,47	33	< 0,001
He > KRM	2,45	11	0,032	He > KRM	2,85	24	0,009
NBC > KRM	4,87	3	0,017	dP ₄ LW	2,35	16	0,032
NBC > ZW	5,47	4	0,005	He > Hn	4,88	46	< 0,001
NBC > ZW	2,67	5	0,044	He > UND	2,89	17	0,010
dP ₃ MW	4,86	24	< 0,001	HeFF > HeMM	2,75	8	0,025
He > Hn	2,42	21	0,025	P ₂ EW	2,93	40	0,006
He > ZW	3,32	7	0,013	He > Hn	2,42	11	0,034
He > NBC	3,70	4	0,021	NBC > Hn	2,76	10	0,020
dP ₃ LW	2,76	12	0,017	P ₂ MW	10,34	55	< 0,001
He > Hn	5,90	3	0,010	He > Hn	3,55	27	0,001
He > KRM	6,54	4	0,003	He > KRM	3,07	27	0,005
NBC > Hn	3,74	27	0,001	He > ZW	2,65	41	0,011
dP ₄ LW	2,47	23	0,021	He > NBC	2,10	25	0,046
He > Hn	2,34	13	0,036	He > Hnv	4,81	48	< 0,001
He > KRM	16,29	2	0,004	NBC > Hn	2,26	34	0,031
HeMM > HeFF	3,08	9	0,013	ZW > Hn	3,44	3	0,041
dP ₂ NW	2,37	7	0,049	P ₃ MW	5,06	10	< 0,001
NBC > KRM	5,51	34	< 0,001	NBC > HTN	2,60	5	0,048
dP ₂ MW	2,98	4	0,041	P ₃ LW	4,59	5	0,006
He > KRM	4,89	32	< 0,001	He > Hn	3,46	5	0,018
He > Hn				NBC > He	2,77	5	0,039
dP ₂ LW				NBC > Hn			
dP ₃ EW				UND > Hn			
He > Hn				MHB > Hn			
dP ₃ LW				P ₄ NW			
He > Hn				He > Hn			

	t	df	p		t	df	p
P ₁ EW	9,97	54	< 0,001	M ₁ LW	3,24	26	0,003
He > Hn	2,31	28	0,029	He > Hn	4,52	4	0,011
He > KRM	4,24	32	< 0,001	HeFF > HeMM	2,21	18	0,041
ZW > Hn	3,52	34	< 0,001	Hnv > Hn	2,28	24	0,032
KRM > Hn	4,48	31	< 0,001	KRM > Hn	2,77	19	0,012
NBC > Hn	2,73	5	0,041	NBC > Hn			
NBC > KRM				M ₂ NW			
P ₄ MW	5,84	19	< 0,001	He > KRM	6,27	14	< 0,001
He > Hn	2,99	5	0,031	He > EFT	2,63	12	0,022
He > Hnv	3,43	5	0,019				
He > KRM	7,80	2	0,016	M ₂ EW	5,68	29	< 0,001
ZW > Hnv	10,75	2	0,009	He > Hn	5,78	17	< 0,001
ZW > KRM	4,58	16	< 0,001	He > KRM	5,09	12	< 0,001
ZW > Hn	3,03	15	0,008	He > EFT	3,12	11	0,010
EFT > Hn	3,00	16	0,008	OAK > He	3,90	18	0,001
BMB > Hn				OAK > Hn	4,32	6	0,005
P ₄ LW	6,83	15	< 0,001	OAK > KRM			
He > Hn	3,76	9	0,005	M ₂ MW	10,69	76	< 0,001
He > KRM	2,69	8	0,028	He > Hn	6,17	37	< 0,001
He > NBC				He > ZW	3,87	45	< 0,001
M ₁ NW	3,39	8	0,009	He > KRM	6,54	36	< 0,001
ZW > KRM	2,71	8	0,027	He > EFT	2,72	33	0,010
UND > KRM				He > BMB	4,44	33	< 0,001
M ₁ EW	2,83	13	0,014	He > EC	3,55	40	0,001
He > Hn	2,19	13	0,047	He > NBC	2,07	55	0,043
He > KRM	2,46	15	0,026	KRM > Hn	2,72	7	0,030
NBC > He	4,16	8	0,003	ZW > EFT	3,35	3	0,044
NBC > Hn	3,60	8	0,007	OAK > EFT	11,23	4	< 0,001
NBC > KRM				MHB > EFT	22,73	5	< 0,001
M ₁ MW	10,84	91	< 0,001	MHB > ZW	2,34	8	0,047
He > Hn	6,11	56	< 0,001	MHB > NBC	5,43	2	0,032
He > KRM	3,60	48	0,001	MHB > Hnv	2,41	50	0,020
He > EFT	4,94	49	< 0,001	NBC > Hn	4,05	4	0,015
He > ZW	3,55	56	0,001	BMB > EFT	2,43	44	0,019
He > NBC	3,34	59	0,001	Hnv > Hn	2,84	4	0,001
NBC > Hn				Hnv > EFT			

	t	df	p			t	df	p
M ₂ LW				P ² LW				
He > Hn	9,20	9	< 0,001	He > Hn		4,89	17	< 0,001
He > KRM	5,11	5	0,004	KRM > Hn		3,96	10	0,003
He > HTN	5,11	5	0,004	NBC > Hn		2,28	10	0,046
M ₃ NW				EC > Hn		2,94	8	0,019
He > KRM	6,51	3	0,007	P ³ NW				
NBC > KRM	28,29	1	0,022	He > Hn		4,60	5	0,006
M ₃ EW				P ³ EW				
He > Hn	4,28	52	< 0,001	He > Hn		9,29	62	< 0,001
He > KRM	6,40	23	< 0,001	NBC > Hn		3,99	33	< 0,001
Hn > KRM	3,36	35	0,002	KRM > Hn		3,26	34	0,003
NBC > KRM	4,16	7	0,004	P ³ MW				
NBC > Hn	2,06	36	0,047	He > Hn		5,53	29	< 0,001
M ₃ MW				ZW > Hn		3,45	18	0,003
He > Hn	4,149	36	< 0,001	NBC > Hn		4,97	18	< 0,001
He > ZW	4,33	18	< 0,001	KRM > Hn		2,82	19	0,011
He > KRM	4,49	19	< 0,001	P ³ LW				
He > EFT	4,37	17	< 0,001	He > Hn		7,60	17	< 0,001
He > EC	2,34	14	0,035	He > KRM		3,09	10	0,011
Hnv > ZW	6,71	5	0,001	NBC > Hn		5,38	11	< 0,001
Hnv > EFT	6,91	4	0,002	ZW > Hn		3,41	8	0,009
Hnv > KRM	3,88	6	0,008	EFT > Hn		2,90	8	0,020
M ₃ LW				EC > Hn		3,11	8	0,015
He > Hn	3,19	8	0,013	UND > Hn		2,38	8	0,044
He > KRM	3,61	6	0,011	P ⁴ EW				
P ² EW				He > Hn		7,19	61	< 0,001
He > Hn	5,47	61	< 0,001	He > KRM		6,03	41	< 0,001
NBC > Hn	3,61	37	0,001	He > NBC		2,65	43	0,011
P ² MW				NBC > KRM		2,29	19	0,034
He > Hn	5,82	27	< 0,001	P ⁴ MW				
He > Hnv	2,78	13	0,016	He > Hn		7,84	24	< 0,001
ZW > Hn	3,13	16	0,006	He > Hnv		4,59	10	0,001
ZW > Hnv	11,25	2	0,008	He > NBC		4,94	9	0,001
NBC > Hn	3,87	15	0,002	He > KRM		3,24	10	0,009

	t	df	p		t	df	p
P ¹ LW				He > EFT			
He > Hn	5,24	21	< 0,001	CS > KRM	4,04	11	0,002
ZW > Hn	2,89	11	0,015	CS > EFT	6,74	4	0,003
KRM > Hn	3,96	10	0,003		12,59	1	0,050
NBC > Hn	4,93	11	< 0,001	M ² EW			
NBC > He	2,24	12	0,045	He > Hn	2,28	29	0,030
UND > Hn	4,18	10	0,002	He > KRM	2,98	18	0,008
UND > He	2,37	11	0,010	He > NBC	4,67	23	< 0,001
M ¹ EW				He > EFT	2,76	18	0,013
He > KRM	3,00	13	0,010	Hn > KRM	2,51	13	0,026
He > Hn	2,49	11	0,030	Hn > NBC	3,33	18	0,004
He > EFT	2,27	10	0,047	Hn > EFT	2,20	13	0,046
M ¹ MW				CS > NBC	3,11	6	0,021
He > Hn	11,70	11	< 0,001	CS > Hn	2,27	12	0,043
He > KRM	6,03	69	< 0,001	M ² MW			
He > HTN	3,34	62	0,001	He > Hn	6,93	105	< 0,001
He > EFT	2,22	62	0,030	He > ZW	3,26	52	0,002
NBC > Hn	4,05	58	< 0,001	He > KRM	7,26	61	< 0,001
NBC > KRM	2,20	16	0,043	Hn > KRM	3,17	64	0,002
UND > Hn	5,01	50	< 0,001	Hnv > Hn	2,51	55	0,015
UND > KRM	4,46	8	0,002	Hnv > ZW	9,62	2	0,011
M ¹ LW				M ² LW			
He > Hn	2,63	40	0,012	He > Hn	5,35	11	< 0,001
HnMM > HnFF	3,62	15	0,003	NBC > Hn	2,87	4	0,045
Hnv > Hn	2,74	21	0,012	MHB > Hn	2,96	4	0,042
ZW > Hn	3,14	21	0,005	M ³ NW			
NBC > He	3,40	24	0,002	He > KRM	5,69	8	< 0,001
NBC > Hn	4,63	24	< 0,001	Hn > KRM	10,39	7	< 0,001
NBC > KRM	2,75	11	0,019	ZW > KRM	13,40	3	< 0,001
KRM > Hn	2,19	27	0,037	NBC > KRM	19,74	4	< 0,001
MHB > He	2,86	20	0,010	NBC > Hn	3,45	5	0,017
MHB > Hn	3,29	20	0,004	M ³ EW			
MHB > KRM	2,75	7	0,029	He > KRM	3,31	33	0,002
M ² NW				He > NBC	2,70	25	0,012
He > KRM	6,44	14	< 0,001	Hn > KRM	4,12	28	< 0,001

M ^s MW									
He > Hn	t	df	p	Hnv > Hn	t	df	p		
He > KRM	4,45	66	< 0,001	Hnv > ZW	5,16	34	< 0,001		
He > EFT	6,63	39	< 0,001	Hnv > NBC	15,88	1	0,040		
He > ZW	2,57	34	0,015	Hnv > KRM	5,64	5	0,002		
He > Hnv	2,28	33	0,029	Hnv > EFT	9,92	7	< 0,001		
Hn > KRM	3,99	34	< 0,001	NBC > KRM	4,72	2	0,043		
	3,57	39	0,001	NBC > ZW	5,95	10	< 0,001		
					2,86	4	0,046		



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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

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DISTRIBUTION AND ECOLOGY OF
THE BLUE ANTELOPE, *HIPPOTRAGUS*
LEUCOPHAEUS (PALLAS, 1766)

VOLUME 65 PART 5

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A NEW GENUS AND SPECIES OF PLIOCENE
BOSELAPHINE (BOVIDAE, MAMMALIA)
FROM SOUTH AFRICA

By
A. W. GENTRY

Cape Town Kaapstad

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By

A. W. GENTRY

British Museum (Natural History), London

(With 28 figures and 4 tables)

[*Ms. accepted 10 July 1973*]

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INTRODUCTION

One of the more remarkable mammalian species from the Pliocene deposits at Langebaanweg in the Cape Province (Hendey 1970*a*, 1970*b*) is a hitherto unknown boselaphine. It is only recently that representatives of this tribe have become known in Africa at all, and this is their most southerly record.

Since reference to the Langebaanweg boselaphine was first made (Gentry *in* Hendey 1970*a*: 114), new material has been recovered and it is now possible to give a more comprehensive account of its characteristics and affinities. All the new material is from Bed 2, 'E' Quarry, and it is probable that the original 'E' Quarry specimens were also from this bed. It is thus an element of a fauna correlated with 4–5-million-year-old East African faunas (Hendey 1970*b*, 1972, 1973).

SYSTEMATICS

Family **Bovidae** Gray

Subfamily **Bovinae** Gill

Tribe **Boselaphini** Simpson

Diagnosis

Tendency for skulls to be lower and wider than in other antelopes; horn cores often with keels but never with transverse ridges, inserted above or just behind the orbits; cranium little angled on axis of the face; braincase not very shortened; frontals between the horn bases generally not far above the level

of the dorsal orbital rims and sometimes with internal sinuses; strong temporal ridges behind the horn cores; small supraorbital pits; low infraorbital foramen; median indentation at the back of the palate behind the level of the lateral ones; posteriorly the ventral edge of the auditory bulla passes upwards to meet the paraoccipital process; entire occipital surface in one plane facing backwards; brachyodont cheek teeth; rugose enamel; lower molars generally without anterior transverse folds (goat folds); long premolar rows; I_{1s} more enlarged than the other incisors or the incisiform canine; depth of mandible beneath the molars does not greatly exceed that beneath the premolars. (Modified from Gentry 1970: 245.)

Remarks

Boselaphini are bush or open woodland antelopes. The only two living forms are inhabitants of the Indian subcontinent: the nilgai *Boselaphus tragocamelus* (Pallas, 1766) and the much smaller four-horned antelope *Tetracerus quadricornis* (Blainville, 1816), but there are many fossil species in Eurasia particularly in the Siwaliks Hills of India and Pakistan, and it is becoming evident that the tribe has also occurred in Africa in the past. The Langebaanweg boselaphine will be defined as a new genus and species.

Mesembriportax n. gen.

Type species

Mesembriportax acrae n. sp.

Generic Diagnosis

The type species is the only member of the genus, and a diagnosis is given under the species.

Mesembriportax acrae n. sp.

Holotype

L 13101—a skull with mandibles, and associated vertebral column, rib fragments and right scapula (Figs 1, 2, 3, 5, 7, 8, 9, 10, 14, 15).

Referred Material

L 20508—Right mandibular fragment with P_2 to M_3 , left mandibular fragment with M_1 to M_3 , and associated vertebrae, rib fragments, left metacarpal fragment, left femur fragment, left lateral malleolus, left metatarsal, one 1st phalanx and three 3rd phalanges (Figs 10, 11, 21, 22, 23).

L 20509—Skull fragments including the right horn core (Fig. 4).

L 13106—Skull fragments including parts of the right horn core (Fig. 5).

L 20506—Skull fragments including left P^2 and P^4 to M^3 , right M^1 and M^2 , left mandibular fragment with M_1 to M_3 and incompletely erupted P_4 , associated with some fragmentary vertebrae.

L 14251—Left and right horn cores (Fig. 4).

L 3003, L 4657, L 5692, L 5923, L 6587, L 12757, L 12758, L 12812, L 12813, L 13141, L 13193, L 20234—Horn core fragments.

Upper teeth as follows:

L 6450—Left and right P^2 and parts of P^3 ; L 10933—left M^3 ; L 10941/6—right M^1 to M^3 and left P^2 and M^1 ; L 12861—right M^1 and M^2 ; L 12862—left and right M^3 ; L 13111—right P^2 and P^3 ; L 13140—right P^3 and M^2 and other fragments; L 14314—left P^2 ; L 14465—left M^2 and M^3 ; L 20536—left M^3 and other fragments.

Mandibular fragments as follows:

L 6601—With left P_4 to M_3 ; L 11821—with left M_1 and M_2 ; L 12860—with right P_4 to M_3 ; L 13136—with left P_3 to M_1 and part of M_2 ; L 13139—with right P_2 to M_3 ; L 14200—with right M_1 to M_3 and left P_3 ; L 14257—with right P_3 to M_3 and left P_2 and M_1 ; L 20405—with right M_1 and M_2 and parts of P_4 and M_3 ; L 20534—with right M_1 , M_2 and part of M_3 ; L 20538/9—with incomplete left P_4 to M_3 and right P_2 to M_3 .

Lower teeth as follows:

L 10924—Left M_1 and M_2 ; L 10936—left P_2 ; L 11979—right P_4 ; L 12698—right M_2 .

The following are juvenile remains:

L 11000/2—Left mandibular fragment with dP_2 to dP_4 , M_1 and M_2 , and unerupted P_3 and P_4 ; right dP_4 , M_1 to M_3 , and unerupted P_2 to P_4 .

L 14202/3—Left mandibular fragment with dP_4 and unerupted M_1 and left maxillary fragment with crushed dentition.

L 14237—Left mandibular fragment with dP_4 and unerupted M_1 .

L 20688—Left and right mandibular fragments with dP_2 to dP_4 and incompletely erupted M_1 ; left maxillary fragment with dP^2 to dP^4 and incompletely erupted M^1 . This material is possibly associated with a number of postcranial bones found nearby (Figs 12, 13).

Tentatively referred material

L 13197—Left scapula (Figs 16, 17).

L 13071—Right humerus, radius, ulna, scaphoid, lunate and metacarpal (Figs 18–22).

L 7625 —Right metatarsal (Figs 21, 22).

L 20334—Right metatarsal.

L 14081—3rd phalanx.

The holotype and all other material is housed in the South African Museum, Cape Town.

Locality

Bed 2 of 'E' Quarry, Langebaanweg, Cape Province. In addition, a single horn core fragment (L 1588A) has been recorded from Baard's Quarry, Langebaanweg.

Age

Pliocene.

Diagnosis

A moderate to large-sized boselaphine; horn cores rather short, inserted fairly uprightly and widely apart, very divergent basally and slightly less so distally, strongly compressed medio-laterally and with a postero-lateral keel and a strong slightly helical anterior keel in their lower part, the anterior keel being stepped at its top and the succeeding distal part of the horn core being of small circular cross-section. Frontals extensively hollowed internally, and their top surface raised much above the level of the top of the orbits; braincase slightly angled on the face axis; top of braincase not curved downwards posteriorly above the occipital surface; strong temporal ridges on braincase roof approaching posteriorly and with a rugose surface between them; braincase widening posteriorly; orbits without a projecting dorsal rim; small supraorbital pits; nasals long and narrow with large central flanges anteriorly but no lateral flanges; large preorbital fossa; infraorbital foramen low and situated above the posterior margin of P^2 ; premaxillae narrow anteriorly but with strong ascending rami of approximately even width throughout and with a wide contact on the nasals; palate very wide; median indentation at the back of the palate well behind the level of the lateral indentations; large mastoid exposure of periotic; anterior tuberosities of basioccipital fairly wide apart and not very large.

Brachyodont or only moderately hypsodont cheek teeth, with not very rugose enamel; small basal pillars on upper and lower molars; medial lobes of upper molars not joined to one another or to the lateral side of the tooth until late in life; mesostyles quite strong on upper molars; central cavities of upper molars not very complicated in outline; medial walls of lower molars rather flat; lower molars sometimes with small goat folds (a transverse flange at the front of the tooth); long premolar rows with large anterior premolars; paraconid and metaconid not fused or only just fused on P_4 ; projecting hypoconid on P_4 ; I_1 s not greatly enlarged.

Name

The generic name is made from μεσημβρινός (mesembrinos) southern, and πόρταξ (portax) a calf, the latter word being a frequent constituent of boselaphine names. The specific name is from ἀκρα (acra) a cape, and is given as a Latinized genitive singular.

The Skull

The holotype skull is largely complete, but owing to some distortion in the facial region it is in three separate parts—the cranium with horn cores, the



Fig. 1. L 13101, holotype of *Mesembriportax acrae*. Lateral view of cranium.
Scale in all photographic figures is in centimetres.

palate, and the remainder of the face region. Part of the occipital, the auditory bullae and other more delicate parts of the basicranium are lost, as is much of the right horn core and parts of the left. Some pieces, especially of the frontals, could not be restored to the skull. The dentition is complete except for some small pieces missing from the upper and lower cheek teeth.

The horn cores are large, without transverse ridges, not curved backwards, and inserted above the back of the orbits. They have an ovate cross-section in their basal part. The anterior keel is very pronounced, and terminates well below the tip of the core. The torsion in the horn cores is anticlockwise from the base up on the right side, and it results in the termination of the anterior keel being situated at what has become the lateral edge of the horn core. Proximally the keel becomes very sharp-edged, a feature which is best seen in the specimen L 13106. The postero-lateral edge is also keeled, while the postero-

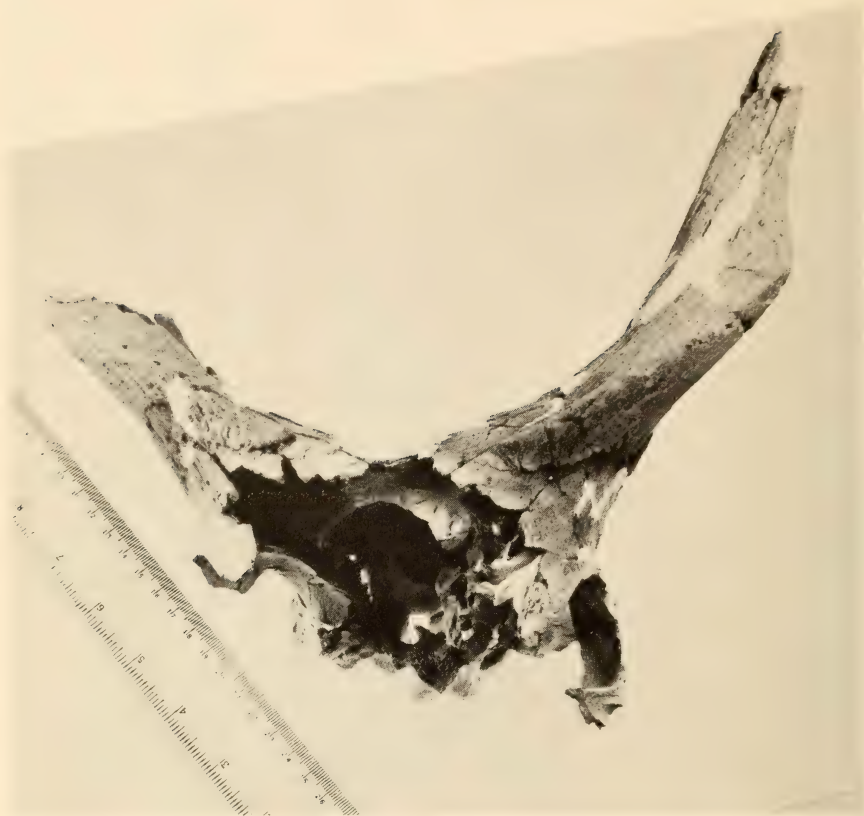


Fig. 2. L 13101, holotype. Anterior view of cranium.

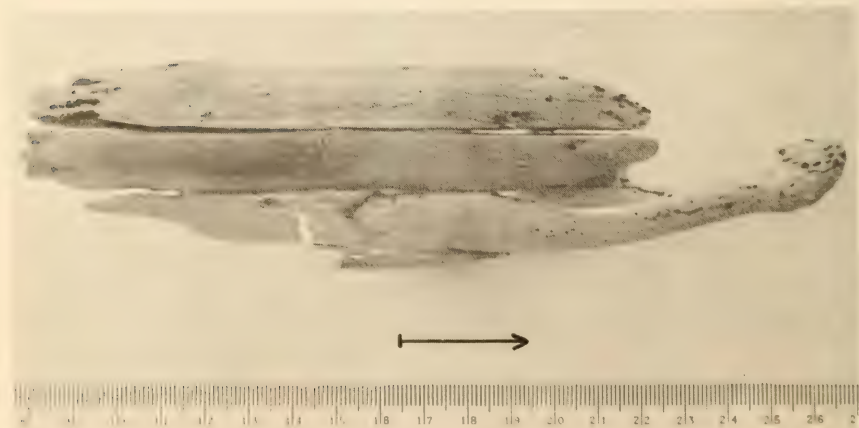


Fig. 3. L 13101, holotype. Dorsal view of nasals with right premaxilla and part of right maxilla; the arrow points anteriorly.

medial edge is rounded. There is some individual variation in shape of the proximal parts of the horn cores; in the holotype and others the medial and lateral surfaces of the lower part of the horn cores are slightly convex and widely angled on the posterior surface, which is also convex, but in L 13106 the postero-lateral keel is more prominent, the posterior surface less rounded, and the lateral surface flatter. In L 4657 and L 20509 there are well-developed grooves running along most of the posterior surfaces of the horn cores. Distally from the termination of the anterior keel the horn core becomes much smaller with a circular cross-section and in this region the horn cores are less widely divergent. The relative length of this distal portion appears to vary considerably as can be seen from Figs 1, 2 and 4.

There are ridges of bone extending antero-medially across the frontals from the anterior keels of the horn cores. Since this region of the skull is incomplete in all specimens it is not known how closely the ridges approach one another. The supraorbital pits are preserved only on the holotype, where they are very small. There is almost no sign of a postcornual fossa postero-laterally to the horn pedicel. The internal hollowing of the frontals extends quite high into the horn pedicel. Extending posteriorly along the midline of the skull from the highest point of the frontals between the horn cores is a ridge of bone which terminates at or near the parieto-frontals suture.

Bohlin (1935) argued that the extinct Eurasian boselaphine *Miotragocerus* originally had horn cores of an elongated oval cross-section, and that later species of the genus evolved periodic growth at the anterior base of the horn core to produce a series of steps along the course of a sharp anterior keel. The horn cores acquired greater and greater antero-posterior diameters during the life-span of an individual. These phenomena may not have occurred in all *Miotragocerus*, and *M. browni* and the Samos skulls named *M. curvicornis* (Andree 1926) and *M. recticornis* (Andree 1926) are obviously difficult specimens in which to visualize them. Thenius (1948) commented that this method of horn core growth did not necessitate periodic sheddings of the horn sheath provided that sheath growth was as in other bovids. He thought that a bifurcated sheath like that of the North American pronghorn, *Antilocapra americana*, may have occurred in *Miotragocerus*. There is no indication of steps along the course of the anterior keel in *Mesembriportax acrae*, except just possibly in L 13106, but one can scarcely imagine it not having a bifurcated sheath at the point where the anterior keel disappeared. This, coupled with the very wide divergence of the horn cores, suggests that males would have fought by grappling, a method of combat different from the pushing and neck fighting of living *Boselaphus* (Walther 1958: 358). The four horns of the living *Tetracerus quadricornis* provide a precedent for anomalous horn features among the Boselaphini.

The thick frontals with their extensive internal sinuses are one of the most notable characters of *M. acrae*. Such sinuses and struts occur in the males of advanced species of Caprini, and help to protect the brain from the ramming and clashing of the very large horns (Schaffer & Reed 1972: 47). In *M. acrae*

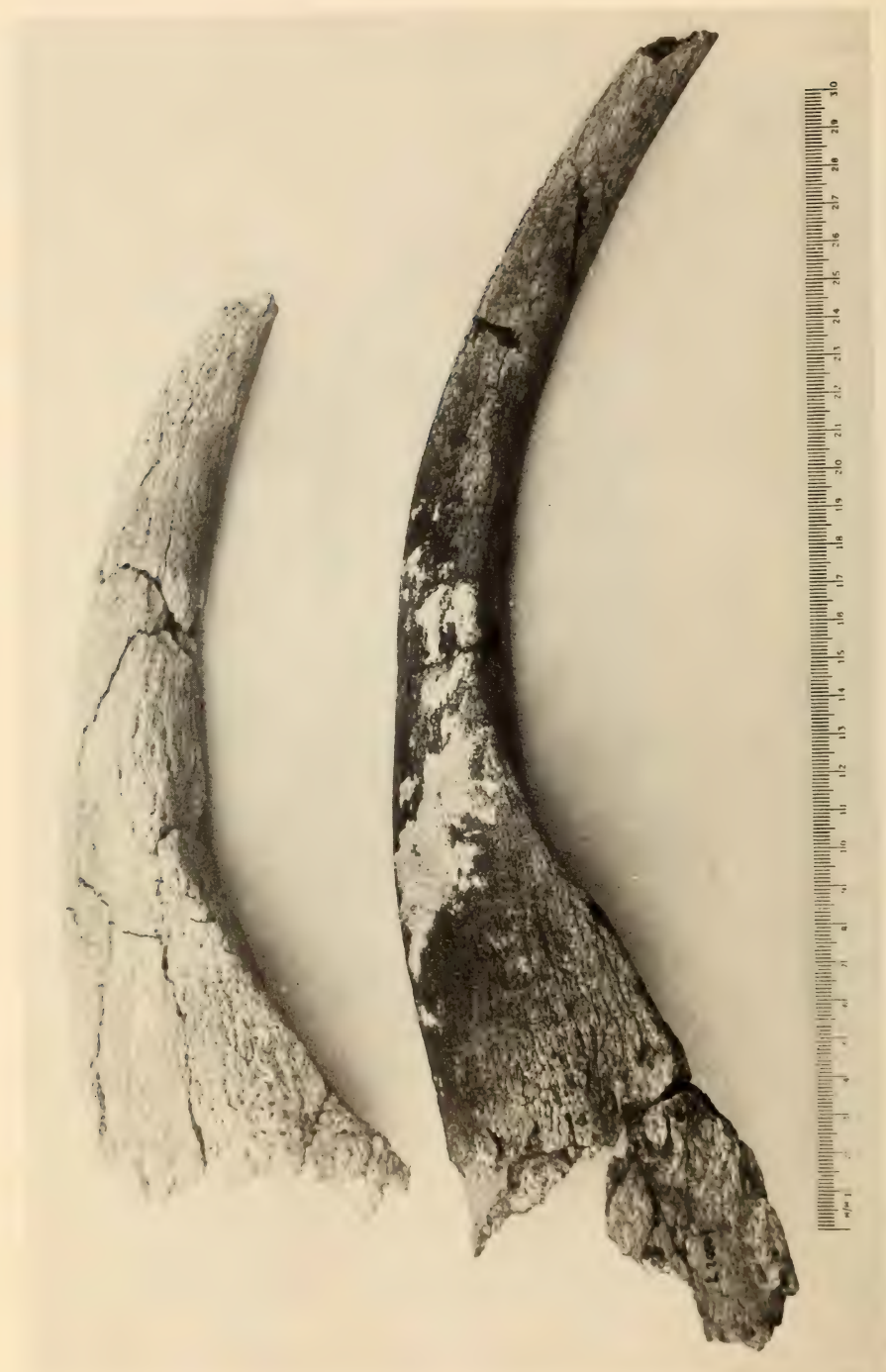


Fig. 4. Antero-lateral views of right horn cores L 14251 (on the left) and L 20509 (on the right).

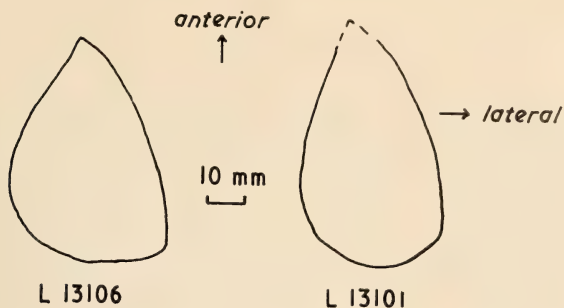


Fig. 5. Cross-sections of two horn cores near their bases.

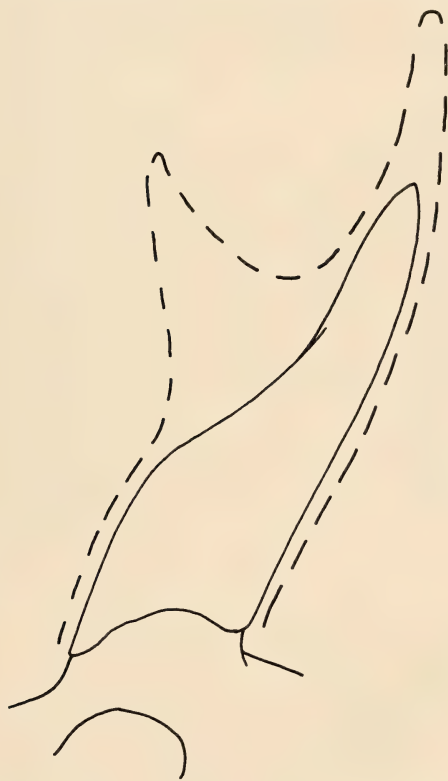


Fig. 6. Diagram of a bifurcated horn sheath (dashed lines) fitted over a horn core of *Mesembriportax acrae*.

they may have protected the brain against the hypothetical horn prongs but were more probably connected with the support of the very divergent and overhanging horns. Such divergent horns may have needed additional bracing to prevent them being too easily snapped during the grappling and pushing between males. The dorso-ventral height of the frontals, irrespective of whether or not

they possessed sinuses, may also have been a means of raising the horns above the level of the orbits, thus giving some protection to the eyes and avoiding interference with the field of vision.

It is not known whether or not the females of *M. acrae* had horns; if the species were like other boselaphines in which the state of this character is known, they did not.

The temporal ridges of *M. acrae* arise from the postero-medial edge of the horn core pedicels, and converge towards the nuchal crest, although they remain fairly wide apart at their posterior termination. The roof of the braincase is flattened in the nuchal region. Arising from the temporal ridges about midway along their length and extending postero-medially are two swellings in the bone which converge about half-way along the surface of the braincase. Anteriorly from these swellings about as far as the parieto-frontals suture, the roof of the braincase is slightly concave and there is a marked rugosity of the bone in this region.

The braincase is broad and rather low, and its roof meets the occipital at an angle of approximately 90° . The nuchal crests are not very prominent; laterally they are directed slightly anteriorly and terminate in large, somewhat bulbous paraoccipital processes. The skull is less wide across the occipital surface than across the orbits. The posterior tuberosities of the basioccipital are fairly prominent, but the anterior tuberosities are small, and there is a slight narrowing of the basioccipital anteriorly. A central longitudinal groove is seen only between the posterior tuberosities, and between the anterior tuberosities there is even a central ridge. The middle of the basioccipital is not transversely constricted.

The preorbital fossae are extremely large, and the width of the face on either side of the narrow nasals is about the same as in the premaxillary region. There is a marked flaring outwards of the face from beneath the preorbital fossa to the alveolar margin of the tooth row. Although this is to some extent a character of all boselaphines, it appears to be exceptionally pronounced in *M. acrae*. The palate is very broad, particularly at the molar rows, and the P^4 s are in fact stepped in from the level of the M^1 s.

The upper molars are large and typically boselaphine in morphology, and all have small basal pillars which are variably developed. In some cases there are two individual pillars on each tooth and in others only one. In the holotype the M^3 s have projections from the most postero-lateral parts of the cingulum. This feature has not been noted in any other boselaphine specimen, nor is it present in other Langebaanweg M^3 s. The upper molars are very broad, the M^1 being appreciably broader at its base than it is long, the M^2 being slightly broader than long, and the M^3 having its breadth approximately equal to its length. The joining of the two medial lobes of each upper molar to one another and to the lateral side of the tooth is possibly more advanced than in earlier boselaphines; in the holotype the junction is actually made but is very narrow in each case. The lower molars have small basal pillars decreasing in size from

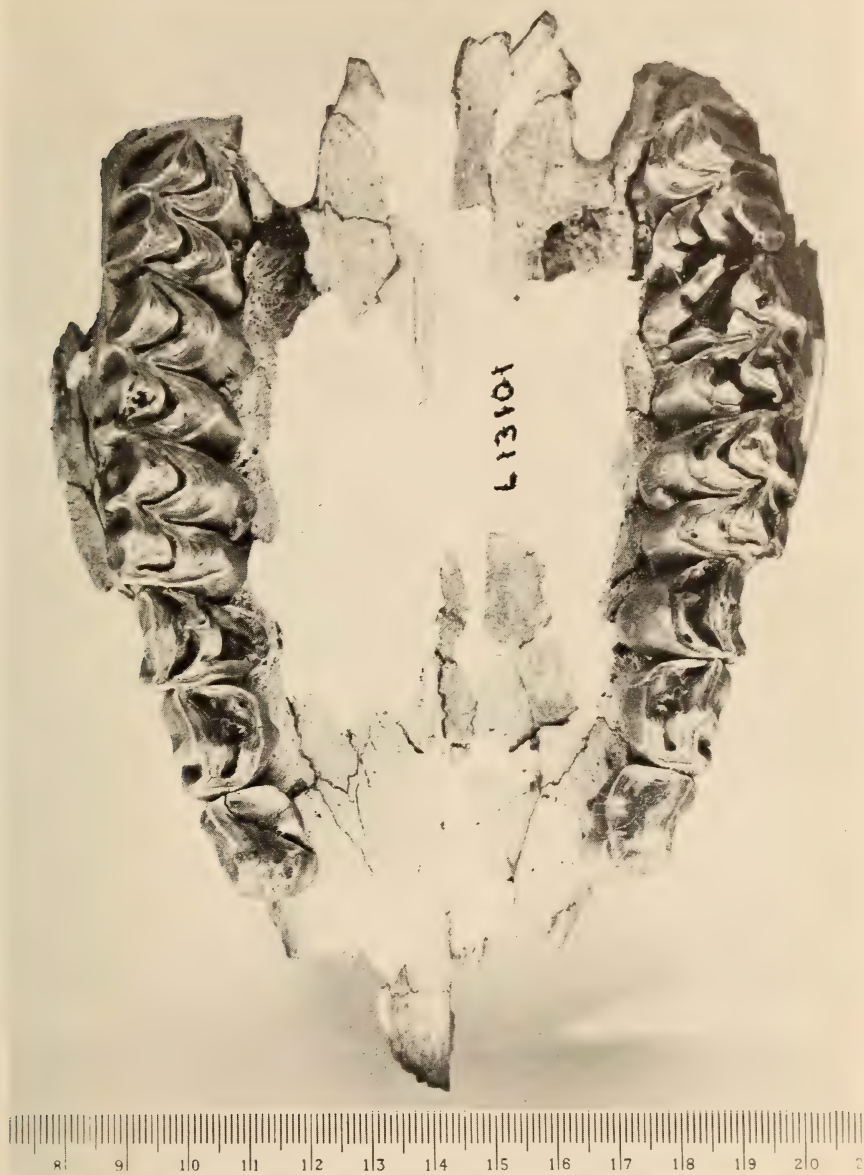


Fig. 7. L 13101, holotype. Palate.

M_1 to M_3 . In the latter tooth there is an additional basal pillar between the middle and the posterior lobes, rather smaller than the main one. The transverse anterior goat folds are poor on the holotype, but stronger in some other lower dentitions which are in an earlier stage of wear, e.g. L 11000. There is a large



Fig. 8. L 13101, holotype. Lateral view of left mandible.



Fig. 9. L 13101, holotype. Occlusal view of left incisors.

metaconid on P_4 and it approaches closely to the paraconid in the holotype but without fusion. In L 20508 the fusion has taken place but is not strong. The central incisors, I_{1s} , are the largest of the symphyseal teeth, but are probably smaller in relation to I_2 , I_3 and C than in the earlier *Protragocerus labidotus* from Fort Ternan, Kenya.

The mandibular diastema is about as long as the lower molar row. The mandibular corpus is relatively shallow and deepens only slightly beneath the tooth row. The ascending ramus rises steeply, almost at right angles immediately behind the M_3 , and its anterior edge and posterior edge below the condyle are nearly parallel. The two anterior deciduous premolars of both the upper and



Fig. 10. Occlusal view of lower dentitions. Above: L 13101, holotype. Below: L 20508.



Fig. 11. Lateral view of left mandible L 20508.

lower dentitions are rather long. The dP^3 is a little-advanced tooth in which the shape of the front lobe is quite dissimilar to the back lobe. The dP_4 has two basal pillars.

The teeth of *M. acrae* agree well with other boselaphines and are not very different from those of Tragelaphini (eland, kudu, bushbuck tribe), so it is reasonable to suppose that this species fed at least partly by browsing. There is a great contrast in almost every character with the teeth of grazing antelopes such as the Alcelaphini (wildebeest and hartebeest tribe).

Measurements in millimetres on the holotype skull are:

Total length of horn core along anterior keel	estimated	370
Total length of horn core along medial curve	estimated	305
Anterior-posterior diameter at base of horn core at right angles to its longitudinal axis		69,1
Latero-medial diameter at base of horn core at right angles to its longitudinal axis		43,1
Minimum width across lateral sides of horn pedicels	estimated	145
Length of nasals	estimated	142
Skull width across mastoids behind external auditory meatus		122
Distance between outer edges of occipital condyles		65,0
Width across anterior tuberosities of basioccipital		26,8
Width across posterior tuberosities of basioccipital		33,0
Minimum width of palate between medial borders of M^3 s		62,5
Occlusal length M^1-M^3		74,6
Occlusal length M^2		27,7
Occlusal length P^2-P^4		55,3
Occlusal length P^2		21,9
Occlusal length P^4		16,0
Occlusal length M_1-M_3		80,7
Occlusal length M_2		24,9
Occlusal length M_3		34,6
Occlusal length P_2-P_4		54,8
Occlusal length P_2		16,1
Occlusal length P_4		20,4
Overall length of mandible from anterior alveolar margin of I_1 to posterior limit of angle	estimated	313
Diastema length	estimated	77,0
Depth of mandibular ramus below P_2		34,0
Depth of mandibular ramus below centre of M_1		40,7
Depth of mandibular ramus below centre of M_3		45,3
Height of ascending ramus between inferior margin and condyle		115

The following additional horn core readings were taken:

	Length along anterior keel	Length along medial curve	Antero-posterior basal diameter	Latero-medial basal diameter
L 4657	—	—	c.65,0	c.41,0
L 13106	—	—	61,7	40,0
L 14251	c.270	c.230	71,5	51,7
L 20509	c.380	c.310	c.74,0	42,4

The distance between the outer edges of the occipital condyles on L 20509 was c.74,0.

Measurements on adult upper teeth were:

L 12861	length M^2	c.26,5		
L 14465	length M^2	27,1		
L 20506	length M^2	24,9	length P^4	13,8

Measurements on lower dentitions are shown in Table 1.

Occlusal lengths of deciduous teeth were:

	dP2	dP3	dP4	dP2-dP4
L 20688 upper	20,9	21,9	21,4	60,1
L 20688 lower	11,8	18,0	28,1	56,4
L 11000 lower	12,7	17,7	c.25,0	—
L 14202 lower	—	—	27,1	—
L 14237 lower	—	—	25,0	—



Fig. 12. L 20688, immature left dentitions. Lateral and occlusal views of mandible with dP₂-M₁.

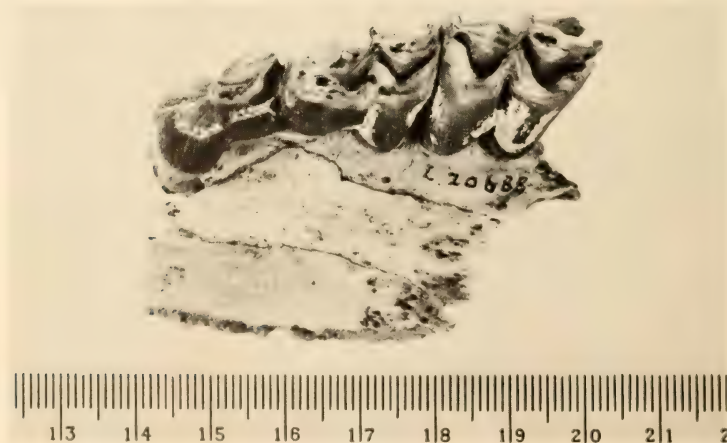


Fig. 13. L 20688, immature left dentitions. Occlusal view of maxilla with dP₂-dP₄.



Fig. 14. L 13101, holotype. Dorsal view of atlas vertebra.



Fig. 15. L 13101, holotype. Lateral view of axis vertebra.

Postcranial skeleton

A large number of bovid postcranial bones has been recovered from Bed 2 in 'E' Quarry, but only a few were associated with *Mesembriportax acrae* cranial remains and thereby positively identified with this species. Apart from



Fig. 16. L 13197, left scapula in lateral view.
See text for explanation of letters in Figs 16-22.

those bones associated with the holotype skull and the cranial elements L 20506 and L 20508, a number of other specimens (L 13197, L 7625, L 20334, L 14081) can be tentatively referred to *M. acrae* because they are very similar to positively identified material. The same applies in the case of a metacarpal which was one element of an incomplete right limb (L 13071). It is possible that L 13071 and



Fig. 17. L 13197, left scapula. Glenoid facet in ventral view.

L 13197 belong to the same individual since they were found close together.

Comparison of the postcranial material with extant antelopes is hampered by the poor samples of the latter—generally not more than two or three individuals of any one species. On their own, none of the fossil postcranial bones can be identified at generic or specific level. In many characters they resemble living tragelaphines, particularly the similarly-sized greater kudu (*Tragelaphus strepsiceros* (Pallas, 1766)), and are distinguishable from comparable elements of alcelaphines. The latter have a morphology suitable for more cursorial forms in an open plains habitat and Gentry (1970: 277–282) has listed and briefly discussed limb bone characters to be expected in such cursorial antelopes. A few cursorial features do appear in *M. acrae*, and it could have been an animal of open woodland. A greater number of cursorial characters appear in the nilgai, also an animal of open woodland, either because it has a slightly different ecological niche, or because it has evolved better adaptations in the last few million years.

The vertebral column associated with the holotype skull is complete as far as the sacrum, comprising seven cervicals, fourteen thoracics and five lumbar. In general the preservation of the individual vertebrae is good although many have lost the processes and other more delicate parts. The atlas and axis are the least well preserved. The atlas has a well-indented dorsal edge anteriorly

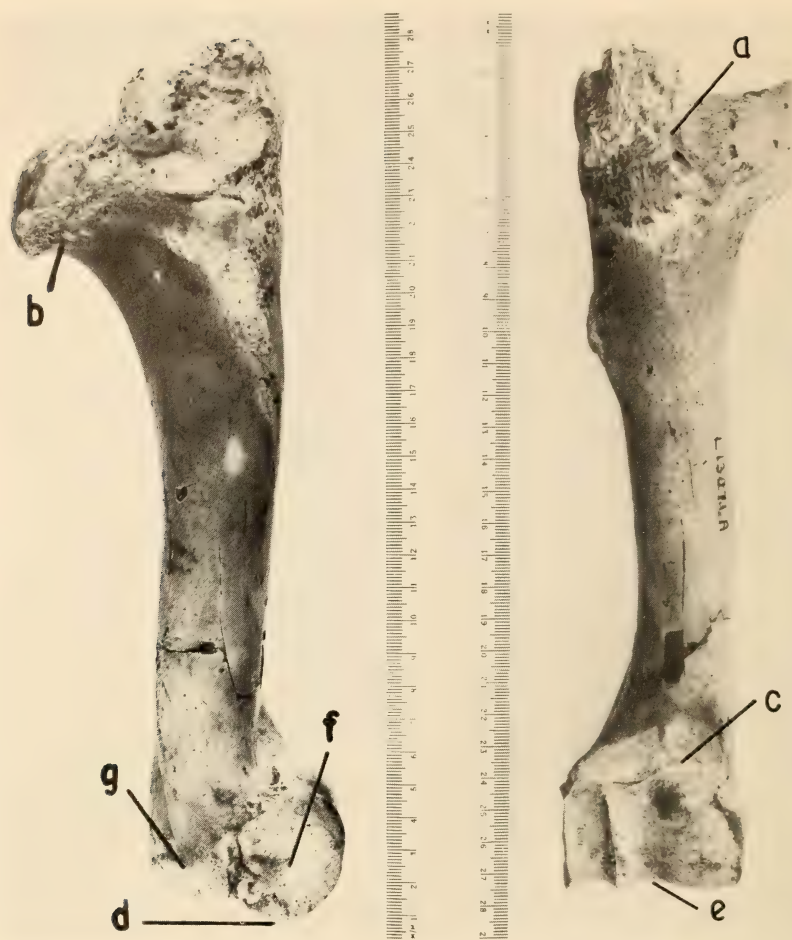


Fig. 18. L 13071. From the left: lateral view of right humerus, anterior view of same.

for articulation with the skull. It is unlike alcelaphines in having no projecting point in the middle of the ventral edge anteriorly, and in having convex rather than concave lateral edges. In these characters it resembles tragelaphines. On the axis the front edge of the neural spine does not pass very far forwards, and on the third and fourth cervicals there are widely separated openings of the vertebrarterial canals. The other vertebrae are not distinctive in any way and those of the referred specimens (L 20506, L 20508) are essentially similar to those of the holotype.

The scapulae of the holotype and the referred specimen, L 13197, have quite small tubera scapulae (a, Fig. 17) in ventral view, with their bases situated above the level of the rims of the glenoid facets in lateral view (b, Fig. 16). The glenoid facets have no indentations in their lateral edges (c, Fig. 17). All these characters

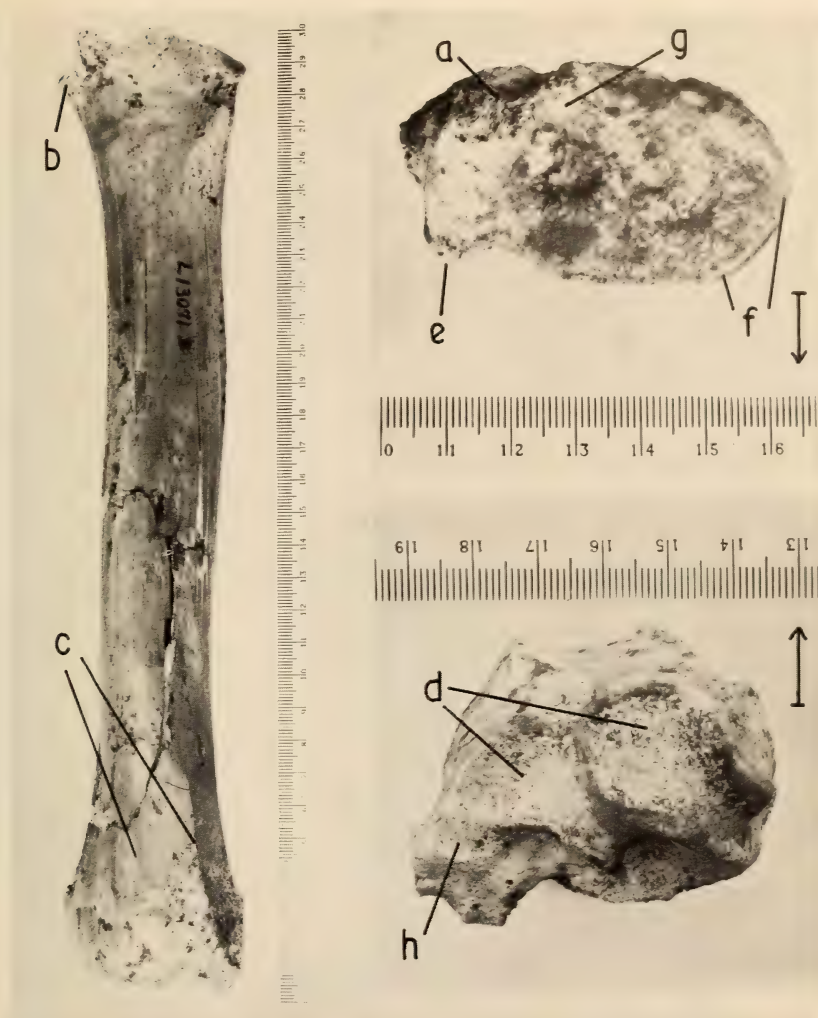


Fig. 19. L 13071, right radius. Left: anterior view. Right above: proximal articular surface.
Right below: distal articular surface.
Arrows point anteriorly.

differ from the condition of alcelaphine antelopes, but the lateral rather than the central position of the tubera scapulae in ventral view (d, Fig. 17) is not unlike alcelaphines. The nilgai has a larger tubera scapulae but is otherwise similar to *M. acrae*.

The humerus L 13071 has the front of its bicipital groove well anterior relative to the level of the front of the lateral tuberosity (a, Fig. 18), scarcely any hollowing for the brachialis insertion under the proximal articular head (b, Fig. 18), no indentation in the dorsal edge of the distal medial condyle

(c, Fig. 18), and no V-shaped ventral projection distally on its lateral side (d, Fig. 18). It is unlike alcelaphines in all these characters. The medial groove of the distal condyle is not very deeply incised (e, Fig. 18) and the distal hollow for the lateral humero-radial ligament is shallow (f, Fig. 18); these characters are also different from alcelaphines and were considered by Gentry (1970: 281) to be expected in non-cursorial bovids. However, the wide bicipital groove, upright distal condyle, and the high distal medial condyle of the fossil are characters of cursorial bovids. The back of the lateral side of the bone does not descend low behind the hollow for the humero-radial ligament (g, Fig. 18). The nilgai agrees with the Langebaanweg fossil only in four characters: the lack of an indented dorsal edge of the medial condyle, the shallow hollow for the humero-radial ligament, the wide bicipital groove and the upright distal condyle.

The radius has the back edge of the proximal lateral facet only a little forward of the level of the back of the medial facet (a, Fig. 19), the proximal lateral tubercle of small to moderate size and set rather low (b, Fig. 19), the distal end of the shaft swollen in lateral view, and wide flanges distally on the anterior surface (c, Fig. 19); all of these characters are unlike alcelaphines and most of them are unlike cursorial bovids generally. However the distal articular facets appear quite deeply incised (d, Fig. 19) to receive the proximal row of carpals, thereby tending to resemble cursorial antelopes. Other characters are a pointed front edge on the proximal lateral facet (e, Fig. 19), no angled medial or antero-medial corners on the proximal medial facet (f, Fig. 19), the postero-medial part of the medial facet projects quite strongly (g, Fig. 19), and the facet for the cuneiform is wide (h, Fig. 19). The nilgai agrees with the Langebaanweg fossil in the swollen distal end of the shaft and the wide flanges on the anterior surface, the deep distal articular facets, the wide cuneiform facet, and the characters of the outline of the proximal medial facet.

The scaphoid is deep, with an upper edge better indented than in the greater kudu but less well than in alcelaphines (a, Fig. 20), and it has no posterior prominence on its medial side (b, Fig. 20). All three characters are unlike alcelaphines, but the first and perhaps the second agree with the nilgai.

The lunate is without a strongly upstanding projection towards the back of its upper surface (c, Fig. 20), and has only shallow hollowings on its lateral (d, Fig. 20) and medial surfaces. Both characters are distinct from alcelaphines and the nilgai.

The metacarpals of L 13071 and that of L 20508, which lacks the lower half of the shaft and distal end, have relatively large unciform facets in comparison with the magnum-trapezoid facets (a, Fig. 22), the total proximal articular surface does not fill the entire available area at the top of the bone, and at the top of the distal condyles there are deep tiny hollows on the posterior surface. These characters are again unlike alcelaphines, and the first and last agree with the nilgai.

The femur of *M. acrae* is known only from a small part of the distal end (L 20508), which is too fragmentary to allow any description of its characters.

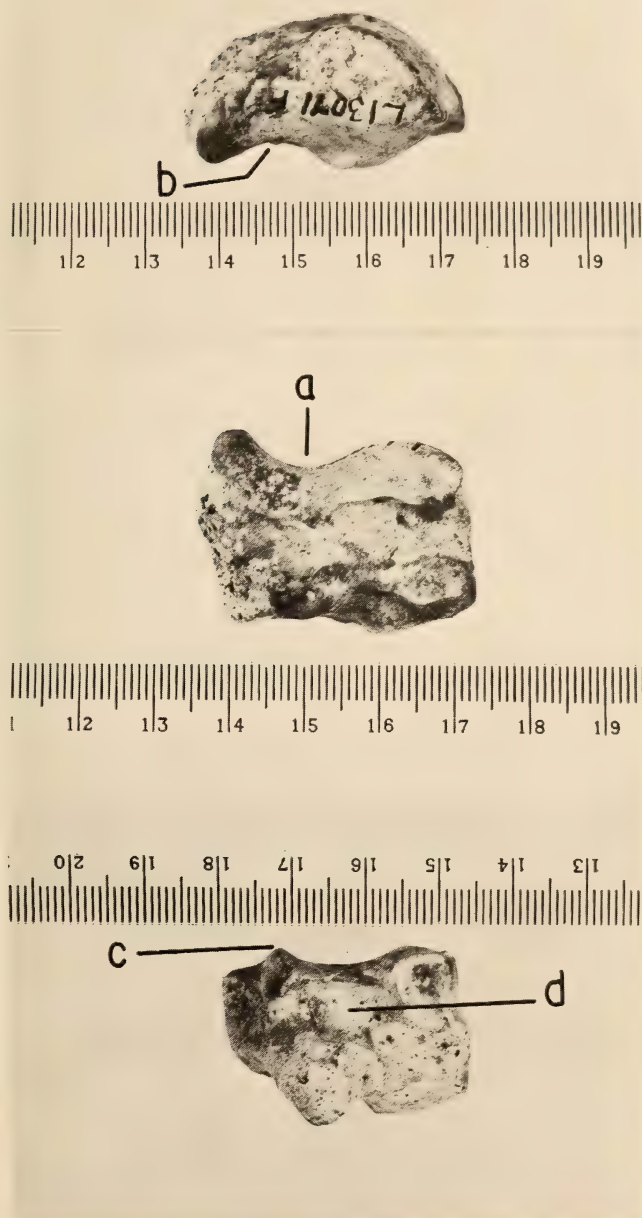


Fig. 20. L 13071. From above: dorsal view of right scaphoid, lateral view of right scaphoid, lateral view of right lunate. Anterior sides lie to the right.

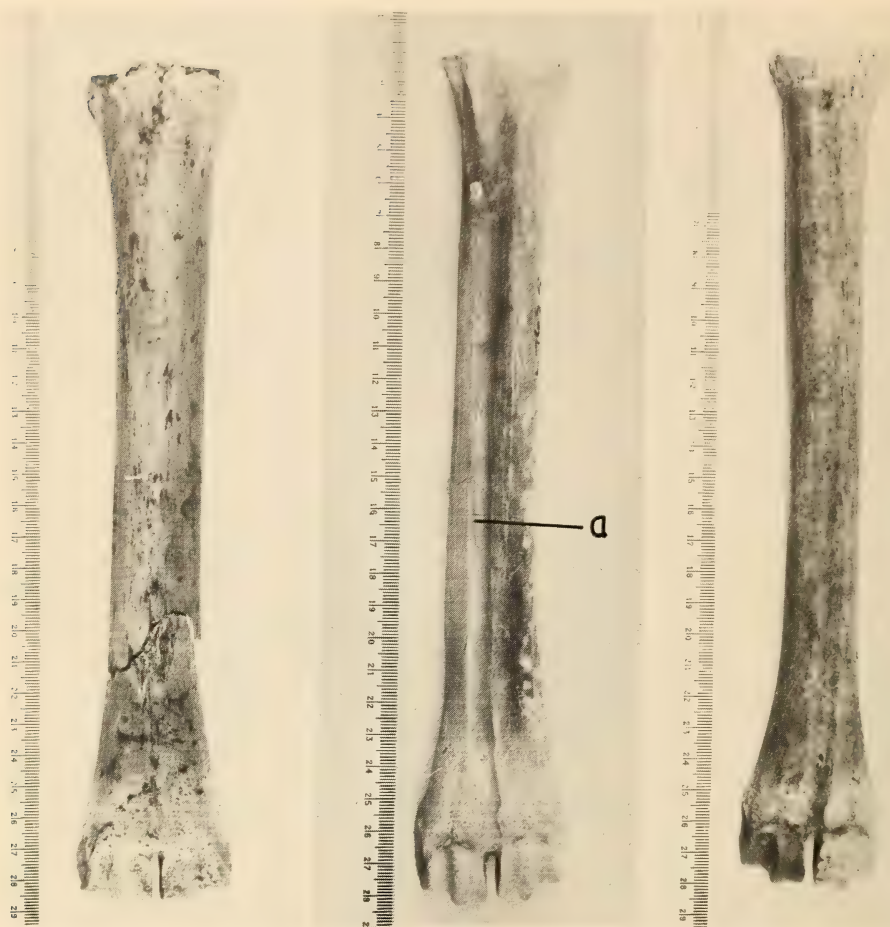


Fig. 21. Anterior views of metapodials. From the left: L 13071 right metacarpal, L 7625 right metatarsal, L 20508 left metatarsal.

The innominate and tibia are not represented by any specimens which can be positively identified with this species and, with the exception of a single lateral malleolus (L 20508), no tarsal bones are recorded either. The lateral malleolus is similar to that of the greater kudu in overall size but is narrower and relatively more elongated antero-posteriorly. It is similar to the lateral malleolus of alcelaphines but unlike the nilgai in that the posterior end of the tibial facet curves ventrally and terminates on the posterior surface of the bone. A secondary, postero-ventrally situated medial facet of articulation with the astragalus is linked to the main grooved facet but is not visible in the nilgai.

The metatarsals of *M. acrae* are more like the metatarsals of tragelaphines than those of alcelaphines. The anterior longitudinal grooves are pronounced and, although their distal termini are medially situated, they are arched along



Fig. 22. Proximal articular surfaces. From above: L 13071 right metacarpal. L 7625 right metatarsal. L 20508 left metatarsal.
Anterior edges lie towards the top of the page.

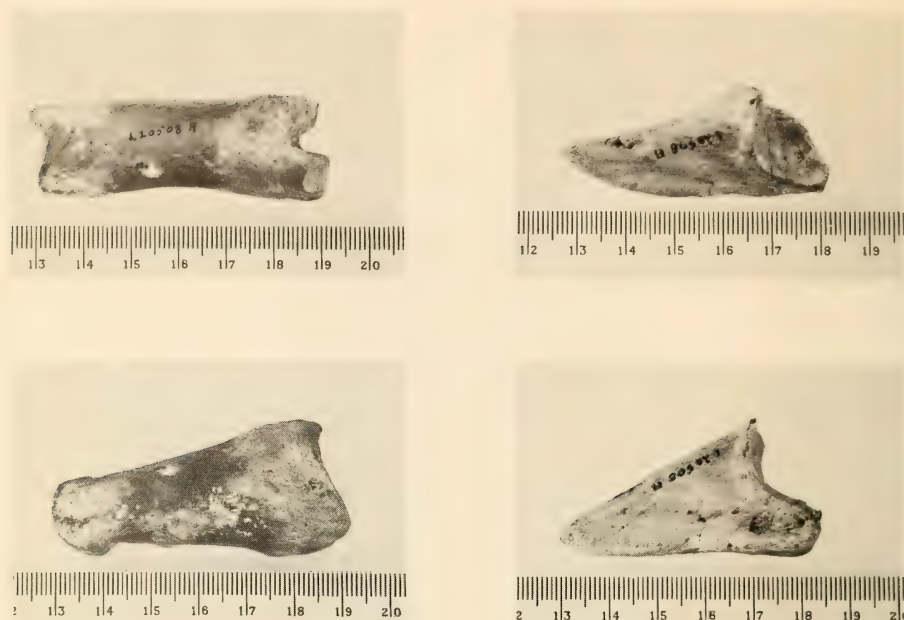


Fig. 23. L 20508. 1st phalanx in dorsal view (above) and outer view (below). 3rd phalanx in dorsal view (above) and outer view (below).

their length towards the lateral edge of the shaft (a, Fig. 21), and their proximal termini are a little off-centre. The metatarsal III elements are thus a more prominent part of the anterior surfaces than the metatarsal IV elements. Tragelaphines, but not the nilgai, also exhibit these characteristics and, although they might be quite pronounced in the eland, the asymmetry is apparently never as extreme as in the *M. acrae* specimens. The secondary (posterior) naviculo-cuboid facets of the proximal surface are transversely elongated (b, Fig. 22) as in the tragelaphines and nilgai, and the posterior part of the articular surface is consequently broader than in alcelaphines and other cursorial bovids (see Gentry 1970: 280). The posteriorly situated facet for articulation with the vestigial metatarsal is more prominent than usual in tragelaphines but less so than in alcelaphines, and thus resembles the nilgai. As in the metacarpal, the posterior hollows above the distal condyles are deep.

The first and third phalanges of *M. acrae* (L 20508, L 14081) are more stoutly proportioned than those of the greater kudu but are not as heavily built as in the eland.

Measurements of the Langebaanweg limb bones are given in Table 2.

Table 2

	Humerus L 13071	Radius L 13071	Metacarpal L 13071	Metacarpal L 12811	Metatarsal L 20508	Metatarsal L 20334	Metatarsal L 7625
Overall length	260,0	c.290,0	c.266,0	c.264,0	270,0	c.254,0	263,0
Maximum transverse diameter at proximal end	75,0	60,5	48,9	51,8	40,1	41,4	39,8
Maximum antero-posterior diameter at proximal end	77,5	33,5	32,2	34,2	38,2	42,0	42,9
Least transverse thickness of shaft	30,5	33,0	c.28,0	—	23,5	—	c.26,0
Maximum transverse diameter at distal end	61,2	56,9	50,2	—	40,5	45,6	47,7
Maximum antero-posterior diameter at distal end	60,7	40,9	33,6	—	31,8	31,8	32,2

The relative lengths of the radius and metacarpal against the humerus, and the least transverse thickness across the shaft of the humerus, radius and metapodials are shown in Figures 24 and 25. In these figures the Langebaanweg bones are compared with the following similarly-sized antelopes:

<i>Tragelaphus eurycerus</i>	bongo	symbol	r
<i>Tragelaphus strepsiceros</i>	greater kudu	„	u
<i>Boselaphus tragocamelus</i>	nilgai	„	n
<i>Connochaetes taurinus</i>	blue wildebeest	„	o
<i>Alcelaphus buselaphus</i>	hartebeest	„	x

The bongo lives in forests, the greater kudu is most typically an inhabitant of hilly country with thickets preferably near rivers, the nilgai lives in areas with scrub or open woodland, and the wildebeest and hartebeest are cursorial antelopes of open plains. In the first three species the humerus is relatively thin and the radius relatively short, and the bongo has a noticeably short metacarpal and a thick radius and metapodials. The metapodials of the wildebeest are thicker than in the hartebeest, and the metacarpal of the hartebeest is notably long. The proportions of the limb bones thought to be of *M. acrae* follow fairly well those of the greater kudu and the nilgai. It is therefore unlikely from this evidence that the species was either a forest inhabitant or a cursorial plains-dweller. More probably it lived in an intermediate habitat of thicket, scrub or open woodland.

COMPARISONS

The tribe Boselaphini belongs to the subfamily Bovinae, which also contains the larger and more specialized Bovini and the African tribe Tragelaphini. Both the latter probably have a boselaphine ancestry. It is clear that *Mesembriportax* is not a bovine or tragelaphine but a boselaphine which developed some specializations of its own and retained some different primitive characters from tragelaphines or bovines. It differs from Tragelaphini by its non-spiralled or scarcely-spiralled horn cores, their medio-lateral compression, the specialized distal part of the horn core, the strong temporal ridges, large preorbital fossa, basioccipital not long or transversely constricted in its centre, and small central incisors. It differs even from the early or primitive bovines *Parabos* Arambourg & Piveteau, 1929 of Europe, *Proamphibos* Pilgrim, 1939 of the Siwaliks, and *Ugandax* Cooke & Coryndon, 1970 of Africa by its smaller size, horn cores with medio-lateral compression and more upright insertions, distal part of the horn core with a sharply reduced cross-section, back of the skull less widened, flatter lateral walls of upper molars and medial walls of lowers, and central cavities of upper molars somewhat simpler.

It differs from the living nilgai, *Boselaphus tragocamelus*, by a wealth of characters, among which it is sufficient to mention the longer horn cores with

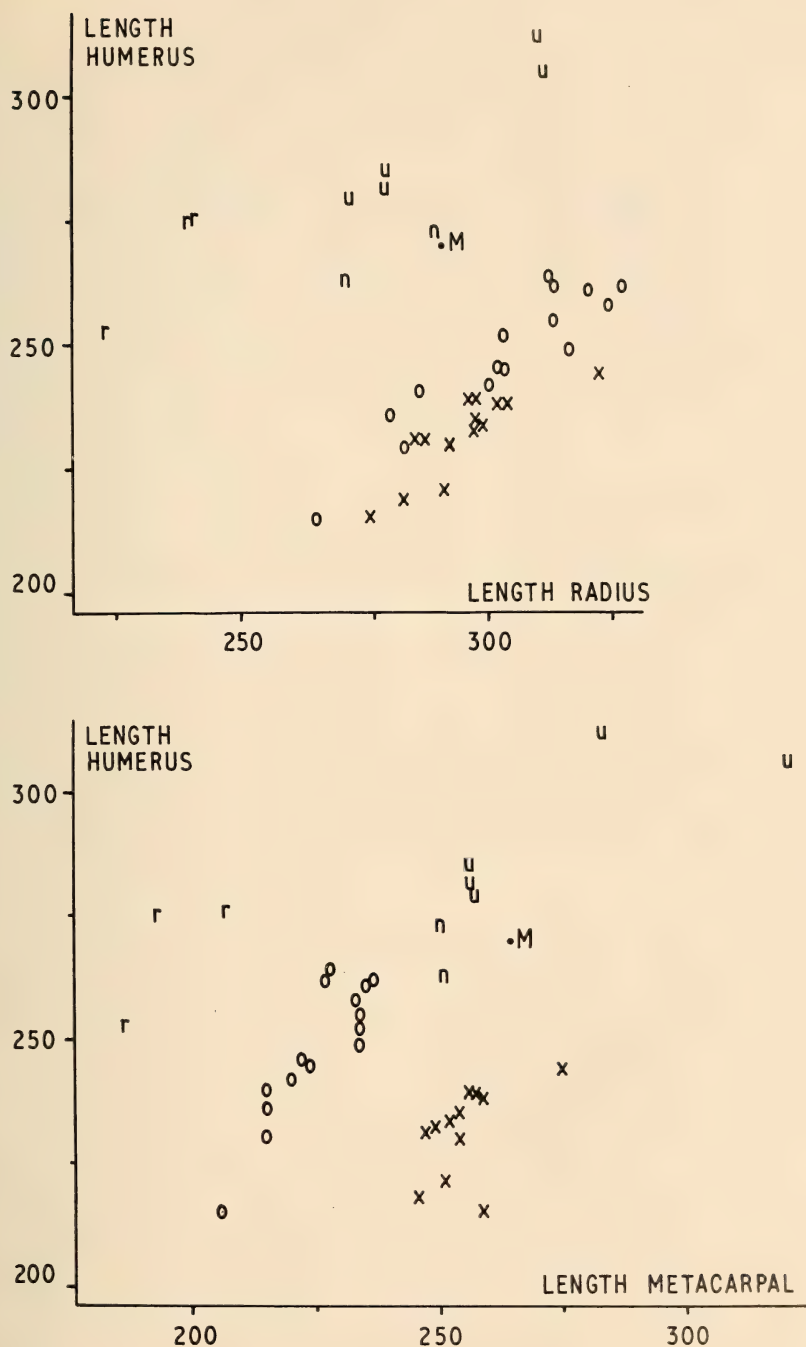


Fig. 24. Graph of humerus length plotted against radius length and metacarpal length. Scales are in millimetres. 'M' marks *Mesembriportax acrae*, and other symbols are explained in the text.

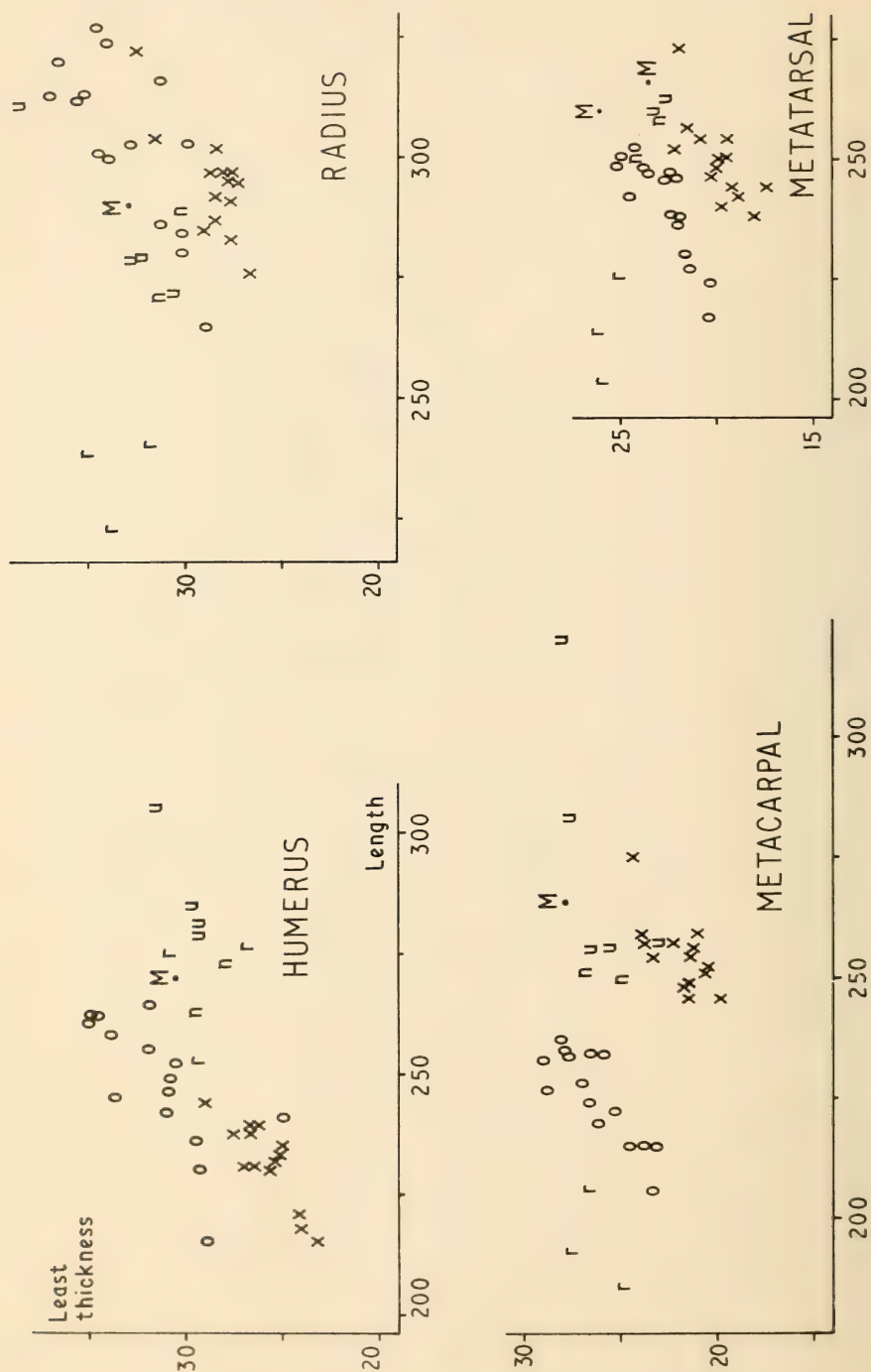


Fig. 25. Graphs of length (horizontal axes) against least transverse thicknesses of the shafts (vertical axes) for four limb bones. Scales are in millimetres, and symbols as in Fig. 24.

an anterior keel ending well below the tip, the horn cores inserted above and not behind the orbits, the extensive sinuses within the frontals, central cavities of molars V-shaped rather than curved, flatter lateral walls of upper molars and medial walls of lowers, longer premolar row and wider premolars, shorter diastema, deeper horizontal ramus of mandible, and fewer cursorial characters in the limb bones. Its much larger size and the possession of only two horns rule out any close relationship to *Tetracerus quadricornis*. Allometry would hinder further comparison between these two forms.

Gentry (in Hendey 1970a: 114) had suggested that the first discovered horn core pieces of *Mesembriportax acrae* might belong to *Miotragocerus* or *Protragocerus*, both of them Upper Miocene boselaphines. The fuller material now available suggests that comparison of *M. acrae* should be made with the following extinct boselaphines:

Pachyportax Pilgrim, 1937

P. latidens (Lydekker, 1876) of the Dhok Pathan and possibly the Tatrot Formations, Siwaliks Hills

P. nagrii Pilgrim, 1939 of the Nagri Formation. Siwaliks Hills

Selenoportax Pilgrim, 1937

S. vexillarius Pilgrim, 1937 of the Nagri Formation

Protragocerus Depéret, 1887

P. chantrei Depéret, 1887 from the European Upper Miocene

P. gluten (Pilgrim, 1937) from the Chinji and lowest Nagri Formations

P. labidotus Gentry, 1970 from Fort Ternan, Kenya and dated to 14 million years (Bishop, Miller & Fitch 1969: 685)

Miotragocerus Stromer, 1928

The more familiar name *Tragocerus*, used until recently for this genus, was discovered by Kretzoi (1968) to be preoccupied by a beetle, and Gentry (1971: 284 footnote) suggested *Miotragocerus* in its place. It contains the following species and perhaps others:

M. gradiens (Pilgrim, 1937) of the Chinji Formation

M. leskewitschi (Borisiak, 1914) of Sebastopol, Russia

M. amalthea (Roth & Wagner, 1854) from Pikermi, Greece, and elsewhere

M. valenciennesi (Gaudry, 1865) a smaller Pikermi and Samos species

M. browni (Pilgrim, 1937) of the Dhok Pathan Formation

M. spectabilis (Schlosser, 1903) of the Chinese mid-Tertiary

Tragoportax Pilgrim, 1937

T. salmontanus Pilgrim, 1937 of the Dhok Pathan Formation

The comparison of *Mesembriportax acrae* with the first two genera of this list is not a matter of difficulty. *Pachyportax nagrii* is a species of only doubtful

validity, having as holotype a hornless female cranium. *P. latidens* is best represented by a cranium, *P.l. dhokpathanensis* Pilgrim, 1939, in Calcutta, of which there is a cast in London. From this it can be seen that *M. acrae* is about the same size as *P. latidens* but has horn cores more strongly compressed medio-laterally, with a stronger anterior keel, inserted more uprightly and having greater divergence. The frontals are raised and have more extensive internal hollowing, the bone surface between the temporal ridges is more rugose, the orbits are without a dorsal rim, the braincase is more angled on the face axis and widens posteriorly, and the nuchal crests are weaker.

Selenoportax vexillarius is a large boselaphine among its contemporaries. The holotype is a cranial roof with horn cores from the Nagri Formation, and only referred teeth are known from the Dhok Pathan Formation. These teeth, along with the holotype juvenile maxilla and referred teeth of a supposed second species *S. lydekkeri* (Pilgrim, 1910), must be regarded as of uncertain identity. *M. acrae* differs from the *S. vexillarius* holotype by its horn cores being shorter, more compressed medio-laterally, with the insertion of the anterior keel not rotated to a medial position, no postero-medial keel, with a reduced circular cross-section in their distal part, the frontals between the horn cores higher than the orbits' dorsal edges, a rugose surface between the temporal ridges, the orbits without projecting dorsal rims, smaller supraorbital pits, the braincase more angled on the face axis, and weaker nuchal crests. The state of internal hollowing in the frontals of *S. vexillarius* is not known, but the available space must have allowed much less than in *M. acrae*. Like *Pachyportax*, *Selenoportax* appears to be an independent boselaphine lineage with no particular relationship to *M. acrae*.

The question of the relationship of *M. acrae* to the last three genera can only be answered within the context of an assessment of how they are related among themselves. *Protragocerus* has been diagnosed by Gentry (1970: 246). It is an early form with such primitive characters as small size, no internal sinuses in the frontals, as much as half of the braincase roof curving downwards posteriorly, no rugosity of the bone surface between the temporal ridges, prominent nuchal crests, and a small basioccipital with but poor development of the anterior tuberosities.

P. labidotus is the most completely known species; it has horn cores with a marked accentuation of their antero-posterior diameter in their lower parts and hence a strong degree of medio-lateral compression, a clearly demarcated terminal portion of the horn core above the top of the anterior keel with a much smaller cross-sectional area, and the horn pedicels becoming extended antero-medially by the development of ridges. *P. labidotus* also shows persisting canine alveoli between the maxillae and premaxillae, and this would probably be seen also in other species were that part of their skulls known. *P. chantrei*, the type species, is very poorly known; it has horn cores with less antero-posterior elongation and hence less medio-lateral compression and less differentiation of a terminal portion, and no ridges on the horn pedicels.

P. gluten, in which Gentry (1970) sank a number of other Siwaliks named forms, needs further interpretation. The holotype and the conspecific cranium of *Strepsiptorax chinjiensis* Pilgrim both have horn cores with a less exaggerated antero-posterior diameter than *P. labidotus*, and are thus less medio-laterally compressed. The main keel at the back is situated postero-laterally. Gentry (1970: 257) synonymized *Helicoportax praecox* and *H. tragelaphoides* with *P. gluten*, but perhaps minimized their differences from the latter. The holotype partial skull of *H. praecox* Pilgrim (1937, figs 6, 7, 62), the holotype horn core of *H. tragelaphoides* Pilgrim (1939, pl. 4 figs 3, 3a), and two other right horn core bases, British Museum (Natural History) M. 15469 and M. 15470, all have larger horn cores than the *P. gluten* holotype (Pilgrim 1937, figs 12–17). In their lower parts the strongest keel at the back is the postero-medial and not the postero-lateral one, and there is more of a transverse ridge across the frontals between the horn bases. Correlated with the strengths of the two posterior keels, the medial surfaces of the horn cores are more flattened than the lateral ones. More distally the postero-lateral keels retain their dominance, and the cross-sections are closer to that of the *P. gluten* holotype. The '*Helicoportax*' specimens may simply be ontogenetically older than *P. gluten*, or they may deserve subspecific rank as *Protragocerus gluten praecox* (Pilgrim). Such a subspecies would not necessarily include the female cranium figured as *H. praecox* by Pilgrim (1937, figs 8–11). If the subspecies is valid, it may be a temporal transition from *P. gluten* to the Nagri *Selenoportax vexillarius* as was thought by Pilgrim himself. It may yet be shown that *P. gluten gluten* survived to give rise to some other boselaphine, such as *Pachyportax latidens*. *Sivoreas eremita* Pilgrim (1939: 131, pl. 4 figs 1, 1a) may belong to *P. gluten*. Gentry (1970: 259) supposed it was antilopine, but was later more doubtful (Gentry 1971: 289). This doubt remains, but while the holotype frontlet and an assigned horn core piece, British Museum (Natural History) M. 15495, show a high degree of spiralling, two other horn core bases, also numbered M. 15495, are rather difficult to distinguish from *Protragocerus*. Certainly there is no case for regarding *S. eremita* as tragelaphine, which was Pilgrim's view.

P. gluten differs from *P. labidotus* by a slightly lower and wider skull, longer horn cores with no basal enlargement of the antero-posterior axis and scarcely any differentiation of the distal portion, and no ridges on the pedicels.

Miotragocerus can be told from *Protragocerus* by its horn cores having less torsion, being inserted less widely apart, sometimes by its higher and narrower skulls, and probably (see Thenius 1951: 278) by having hollowed horn core pedicels. *Miotragocerus leskewitschi* is a species with a number of primitive characters. The downwards curvature of the back of the braincase roof (less pronounced than in *Protragocerus*), the smallness of the basioccipital and its poorly developed anterior tuberosities may be mentioned in particular, and the rather small overall size, short horn cores, and lack of much surface rugosity between the temporal ridges, may also be primitive. Its nuchal crests are not strong, and the tip of the horn core has smaller cross-sectional areas than the

more proximal part. Whether it is actually early for a *Miotragocerus* depends on the dating of Sebastopol, which is discussed in Van Couvering & Miller 1971 and Van Couvering 1972. *M. amalthea* is a larger species with somewhat longer horn cores in which the distal portion has a small cross-sectional area, the frontals have some internal sinuses, and there is an upstanding transverse ridge between the horn pedicel bases. There is still not a great development of surface rugosity between the temporal ridges. The basioccipital is larger than in *M. leskewitschi* and has scarcely any development of a central longitudinal groove. The skull is more definitely low and wide than in *M. leskewitschi* and the horn cores show some degree of torsion, both of which are approaches to *Protragocerus*. *M. monacensis* Stromer and *M. pannoniae* (Kretzoi) are names which have been applied to more north-westerly occurring examples of the genus. Illustrations of them (Stromer 1928, fig. 1; Thenius 1948, figs 1, 2; Tobien & Jörg 1959, pl. 11) show short straight horn cores without much torsion but with terminal portions of abruptly smaller cross-sectional area, stronger rugosity of the bone surface between the temporal ridges than in *M. amalthea*, a little downwards curvatures at the back of the braincase roof, and the premaxilla rising with even width to make contact with the nasals. *M. valenciennesi* is a scarcely known smaller species than *M. amalthea*, found at Pikermi and Samos, and there is also perhaps a larger species at these sites (Gentry 1971: 243). Some *Miotragocerus* at Samos differ from *M. amalthea* in having longer horn cores, with less torsion and most probably with no demarcation of their distal part; they may also have the braincase more angled on the face axis. They have received the names *M. curvicornis* (Andree 1926) and *M. recticornis* (Andree 1926). A similar skull in the American Museum of Natural History, 20566, comes from quarry 5 at Samos, which may be later than other sites on that island (Gentry 1971: 280). *M. gradiens* is a small, primitive-looking species with some similarity to *M. leskewitschi*, but it has a narrower skull and slightly more upright horn cores, both of which must have helped to distinguish it from the contemporaneous *Protragocerus*. *M. vedicus* (Pilgrim 1939: 244) appears very similar to *M. gradiens* but comes from the later Dhok Pathan Formation; possibly it is an ontogenetically young specimen of a later species. *M. browni* (Pilgrim 1937: 781) is a later Siwaliks species apparently smaller than *M. amalthea*, although Pilgrim (1939: 217) was inclined not to stress this. It may or may not be conspecific with *M. punjabicus* Pilgrim, 1910. It has a higher and narrower skull than the European forms, and the holotype shows long horn cores curving backwards and without a terminal portion of small diameter. The rugosity of the frontals is not well marked. *M. spectabilis* of China is not well differentiated from *M. amalthea*.

Tragoportax salmontanus in the opinion of Gentry (1970: 259) includes material of two other supposed species from the Siwaliks. *Tragoportax aiyengari* Pilgrim (1939: 228, fig. 24) was founded on a cranium with horn core bases said to be from the Dhok Pathan Formation. A plaster cast of this cranium is available in London, and it differs from *T. salmontanus* by being larger, having

more upright horn core insertions in side view and a less pronounced transverse raising of the frontals between the horn bases. It does not seem sufficiently different from *T. salmontanus* to justify specific rank. Other Dhok Pathan remains have been referred to *T. islami* Pilgrim (1939: 230, figs 25d-f, 26). The holotype is a partial cranium, of which a plaster cast is available in London. The transverse narrowness of the cranium makes it doubtful that it comes from a *Tragoportax* rather than a *Miotragocerus*, and the remaining horn cores cannot be separated convincingly from *T. salmontanus*. *T. salmontanus* is smaller than *M. amalthea* and has fairly short horn cores probably without a distinct terminal portion, horn cores inserted close together and with an upstanding transverse ridge of the frontals between the bases, internal sinuses of the frontals, a strongly rugose surface between the temporal ridges, the back of the braincase a little down-curved posteriorly, and a basioccipital with a longitudinal groove extending forwards to pass between the anterior tuberosities. *T. salmontanus* is obviously a member of the *Protragocerus*-*Miotragocerus* group, but it is questionable whether it deserves separate generic rank. It is different from *Protragocerus* in the closeness of the horn core insertions, the raised ridge between the pedicels, the lack of a distinct terminal portion of the horn core, the braincase widening posteriorly, the rugosity of the bone surface between the temporal ridges, and the larger basioccipital with its more pronounced central groove. There are fewer differences from *Miotragocerus* which is a more diverse genus.

Mesembriportax acrae differs from *Protragocerus* by its greater size, horn core insertions less inclined backwards, the greater divergence of the horn cores, the internal sinuses of the frontals raising them well above the level of the top of the orbits, no dorsal rim to the orbits, the braincase roof angled and not curving downwards posteriorly, braincase widening posteriorly, a rugose surface between the temporal ridges, and a relatively larger basioccipital with stronger anterior tuberosities. It differs from *P. labidotus* by less extreme compression of the horn cores, the absence of a projecting anterior ridge on the horn pedicels, temporal ridges wide apart posteriorly, weaker nuchal crests, nasals without lateral flanges anteriorly, lower molars with straighter medial walls and occasional incipient goat folds, a longer premolar row (Fig. 26), a more massive metaconid on P_4 , a closer approach of metaconid and paraconid on P_4 , and more reduced canine alveoli at the maxilla/premaxilla junction. Many of these differences can be seen as evolutionary advances: greater size, frontals' sinuses, profile and rugosity of braincase roof, less marked nuchal crests, the basioccipital characters and the disappearance of the canine alveoli. The tooth characters, particularly the relative lengthening of the premolar row, cannot be so easily seen as advances.

Mesembriportax acrae differs from all *Miotragocerus* by having horn cores inserted more widely apart and with greater divergence, more extensive frontals' sinuses, orbits without dorsal rims, and the braincase more angled on the facial axis. It differs from all except *M. amalthea* by its greater size, horn cores with more torsion, and braincase widening posteriorly. It differs from *M. amalthea*

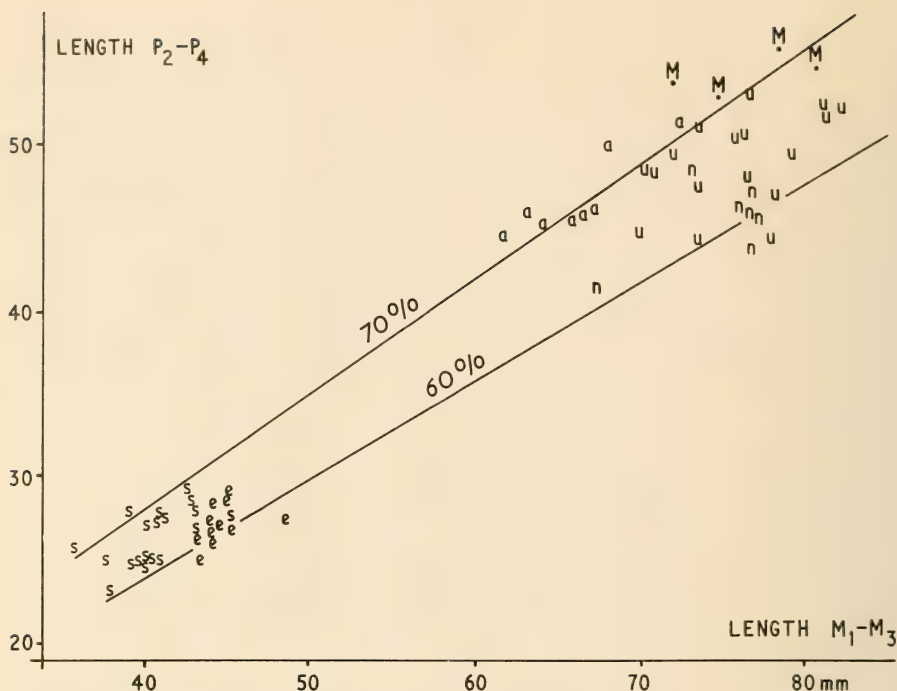


Fig. 26. Graph of length of lower premolar row against lower molar row. *a* = *Miotragocerus amalthea* from Pikermi, *e* = *Protragocerus labidotus*, *n* = *Boselaphus tragocamelus*, *s* = *Tragelaphus scriptus*, *u* = *Tragelaphus strepsiceros*, *M* = *Mesembriportax acrae*. The upper diagonal line passes through points along which the length of the premolar row is 70% of that of the molar row, and the lower one is the corresponding line for 60%.

by having less tendency to a postero-medial keel on its horn cores, and perhaps more of a rugose surface between its temporal ridges. It differs from *M. browni* by the wider skull, shorter horn cores which are less curved backwards, with less of a tendency to a postero-medial keel, and with the anterior keel terminating well below the horn core tip. There are other differences of *Mesembriportax acrae* from the more primitive-seeming *Miotragocerus gradiens* and *M. leske-witschi*. It is interesting that the plate of a *Miotragocerus* skull in Tobien & Jörg (1959, pl. 11) shows a premaxilla rising with even width to make a contact on the nasals, as in *Mesembriportax acrae* and *Protragocerus labidotus*. This bone conformation may be primitive in Boselaphini.

Definitely identified upper and lower dentitions of *Miotragocerus* are known, from which *Mesembriportax acrae* differs by the straighter medial walls of its lower molars. The P_4 of the *M. acrae* holotype differs in its more massive metaconid with less differentiation into a neck and strong anterior and posterior flanges, the paraconid assuming the shape of a low protuberance from the parastylid rather than a flange, and the hypoconid projecting more strongly than in many *Miotragocerus*. However, in L 20508 (Fig. 10) only the

last difference appears valid. The premolar row is about as long as in *M. amalthea* from Pikermi (Fig. 26).

Mesembriportax acrae differs from *Tragoportax salmontanus* by being larger, the top of the anterior keel terminating well below the tip on the horn core, the horn cores inserted more uprightly and further apart, the greater divergence of the horn cores, the expanded internal sinuses of the frontals and the orbits without a projecting dorsal rim, the braincase more angled on the face axis, the braincase roof not curved downwards posteriorly, temporal ridges not approaching so closely posteriorly, and the central longitudinal groove on the basioccipital not extending forwards between the anterior tuberosities.

Mesembriportax acrae seems to be a fairly isolated form by the huge extent of its frontals' sinuses and by other characters of the skull top and horn cores. The wide palate may also be notable. It could perhaps have descended from the Fort Ternan *Protragocerus labidotus*, which has horn cores with quite strong torsion, wide insertions, medio-lateral compression, and a long terminal part of small cross-section. The development of such distinctive horn core tips would be unique outside *Miotragocerus*, and only occurred in an area south of the known range of *Miotragocerus*. The main problems with such a hypothesis of descent are what could have happened to the anterior ridges of the horn pedicels and whether the premolar row could have lengthened. *Mesembriportax acrae* seems rather further from *Miotragocerus*, which has narrower skulls (with the possible exception of *M. amalthea*) and more closely inserted horn cores with generally less torsion. Its wide horn core insertions and the basioccipital morphology suggest that it is not close to *Tragoportax salmontanus*. A tentative phylogeny is shown in Figure 27.

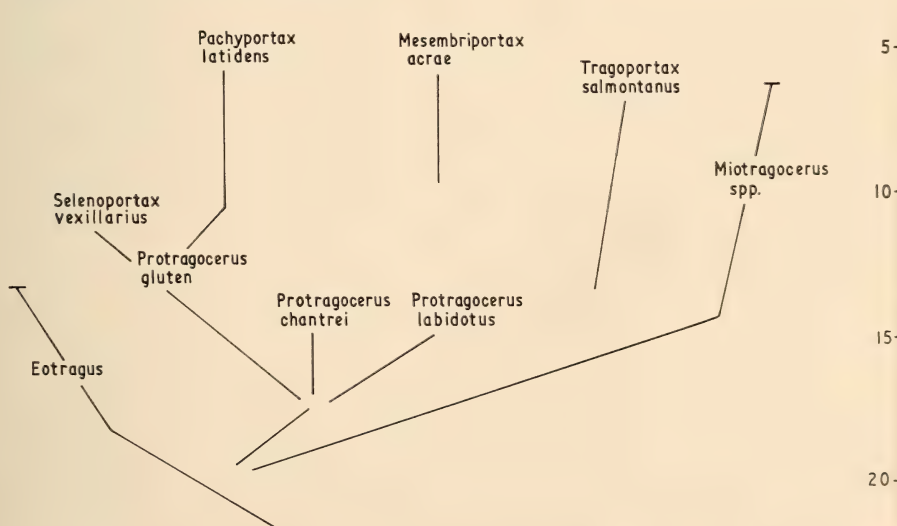


Fig. 27. Phylogeny for some Boselaphini. The time scale is in millions of years. The origins of Bovini, Tragelaphini and the two living boselaphines are too questionable to be shown here.

[illegible]

PHENETIC COMPARISONS

A simple quantitative assessment of the phenetic differences of *Mesembriportax acrae* from other boselaphines was undertaken, slightly modified from the method of Corbet & Hanks (1967: 50). The results of such a straightforward, unweighted morphological comparison, taking no account of time, phylogeny or allometry, are interesting in comparison with the findings just stated above.

Table 3 is a list of non-metrical characters in which the species differ. The data is taken from material and casts in the British Museum (Natural History) and from published illustrations. Tooth characters are omitted since they are available only for *Mesembriportax acrae*, *Protragocerus labidotus*, *Miotragocerus amalthea*, *M. leskewitschi* and the nilgai. The state of the characters in *Mesembriportax acrae* has been designated by a + sign, and the opposite state for each character by a - sign. In the column headed 'state', the first alternative describes the character in *M. acrae*. No allowance has been made for intermediate states, and blank spaces are left where characters cannot be determined on available material. Numerical values can then be given to the character states: + = 1, - = 0, and the sum of differences of *M. acrae* from each of the comparative species is shown at the foot of the columns of Table 3, expressed as a fraction of what the total score would have been if the two species had differed in every character. Normally this total is 25, but the incompleteness of some fossils reduces it to 20 or 22. The fractions are standardized as percentages in the lowest line of the table.

TABLE 4
Percentage differences between pairs of boselaphine species.

	1	2	3	4	5	6	7	8	9	10
1 <i>Boselaphus tragocamelus</i>										
2 <i>Pachyportax latidens</i>	30									
3 <i>Selenoportax vexillarius</i>	32	18								
4 <i>Protragocerus gluten</i>	40	35	41							
5 <i>Protragocerus labidotus</i>	52	35	55	20						
6 <i>Miotragocerus gradiens</i>	59	56	79	32	23					
7 <i>Miotragocerus leskewitschi</i>	56	45	68	24	20	9				
8 <i>Miotragocerus amalthea</i>	44	35	45	28	40	41	28			
9 <i>Miotragocerus browni</i>	40	40	55	40	60	36	40	28		
10 <i>Tragoportax salmontanus</i>	48	55	64	32	36	27	24	28	40	
11 <i>Mesembriportax acrae</i>	48	40	50	48	52	55	48	28	48	40

The top row of numbers indicates the same species as are listed on the left.

The percentage differences were then found between every pair of species in Table 3, and the resulting figures are given in Table 4. Figure 28 shows a dendrogram of phenetic differences based on the percentages in Table 4; in this dendrogram the positions of the linking lines between any two clusters represent the mean difference between all members of one cluster and all members of the other cluster.

Several interesting observations arise from these exercises.

1. According to Table 3, *M. acrae* is phenetically remote from the early genus *Protragocerus*, from three of the four *Miotragocerus* species, from *Selenoportax vexillarius*, and from the nilgai. Percentage differences from all these forms are 48 or above.

2. It is least different from *Miotragocerus amalthea*, being quite pronouncedly closer to it than to any other species. This is a surprising contrast to the hypothesis of descent from a *Protragocerus* species. Even if tooth characters were taken into account, as is possible for these three species, the percentage differences from *M. amalthea* and *P. labidotus* would only change to 31 and 57 respectively. However, Table 4 shows that *M. amalthea* has no large and no small percentage differences from any other species. Its total range of readings extends only from 28 to 45, compared with 9 to 68 for *M. leskewitschi* or 18 to 79 for *Selenoportax vexillarius*. It seems to be very much an 'average' boselaphine. Not only does it have no linkage lower than 28 to any other species, but it links simultaneously with four species at that level. Its closeness to *Mesembriportax acrae* should be judged only in conjunction with these reservations.

3. Tables 3 and 4 confirm that *Mesembriportax acrae* is a well-marked form, and support its attribution to a new genus.

4. Concerning the other species used in the phenetic comparisons and shown in Figure 28, it may be noted that the species pairs *Pachyportax latidens*

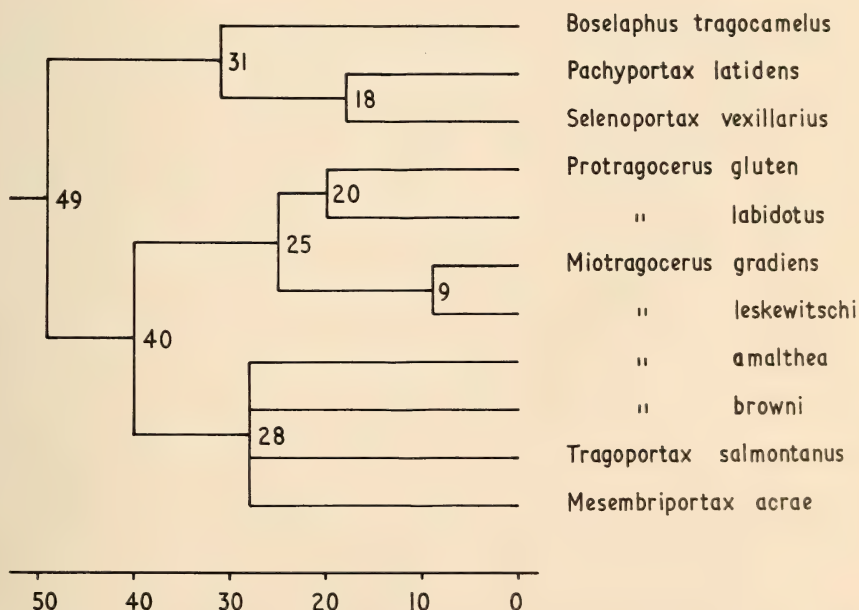


Fig. 28. Dendrogram of phenetic differences between some Boselaphini.

with *Selenoportax vexillarius*, the two *Protragocerus* species, and *Miotragocerus gradiens* with *M. leskewitschi* are convincing or plausible phyletic groupings. The same may also apply to the further link of the nilgai with *Pachyportax* and *Selenoportax*. This takes place at the 31 level, which is quite a lot lower than the nilgai's link with any other species. The complete central cluster joined at 25 is a union of early, primitive or small boselaphines, and this imposes a 'horizontal' rather than a 'vertical' arrangement of species in the rest of the dendrogram. It leaves the bottom four species as a cluster of larger and later or more advanced boselaphines. It is doubtful whether even the two *Miotragocerus* species and *Tragoportax salmontanus* in this later group are phyletically closer to each other than to *M. gradiens* or *M. leskewitschi* in the preceding cluster. Indeed, *T. salmontanus* would have had closer links with *M. leskewitschi* and *M. gradiens* at 24 and 27 respectively had they not already joined *Protragocerus*. The inclusion of *Mesembriportax acrae* in this phenetic group is a clear clash with the phyletic interpretation presented in this paper, and may be attributed to parallel evolution and to the fact that *Miotragocerus amalthea* happens to link with several species at the 28 level.

The numerical phenetic comparison has been useful in emphasizing the close morphological resemblance of *Mesembriportax acrae* to *Miotragocerus amalthea*, but the results of such a comparison must evidently be interpreted very carefully when applied to taxa of different overall body size and different time levels.

CONCLUSION

Mesembriportax acrae has been seen to have several interesting specializations, most notably those associated with the frontals and horn cores. It has very divergent horn cores, possibly with bifurcated sheaths, inserted widely apart on frontals which possess an extensive system of internal sinuses.

It may have descended from a boselaphine like *Protragocerus labidotus*, but in doing so it evolved some cranial characters in parallel with *Miotragocerus amalthea*, well known from the Upper Miocene of Europe.

It has been shown that the morphology of the teeth of *Mesembriportax acrae* agrees broadly with the boselaphines and tragelaphines, but that the premolar row is rather long, particularly in comparison with the nilgai. This might indicate a wholly rather than a partly browsing diet. The limb bone proportions are nearer to both nilgai and greater kudu than to antelopes of open plains or thick forests, and the morphology of the limb bones is more like the greater kudu than the nilgai. So far as can be judged from written comments, the nilgai may differ ecologically and behaviourally from the greater kudu by living in terrain which is less hilly and more open, and by being partially a grazer instead of predominantly a browser (Prater 1965: 273; Schaller 1967: 171; Dorst & Dandelot 1970: 194; Wilson 1965). It is possible that *M. acrae* was nearer to the greater kudu pattern of life. However, as a Pliocene antelope it could have had less highly evolved adaptations for a nilgai-like ecology.

SUMMARY

Some well-preserved fossils of a new genus and species of a boselaphine antelope, *Mesembriportax acrae*, are described from the Pliocene of Langebaanweg, Cape Province, South Africa.

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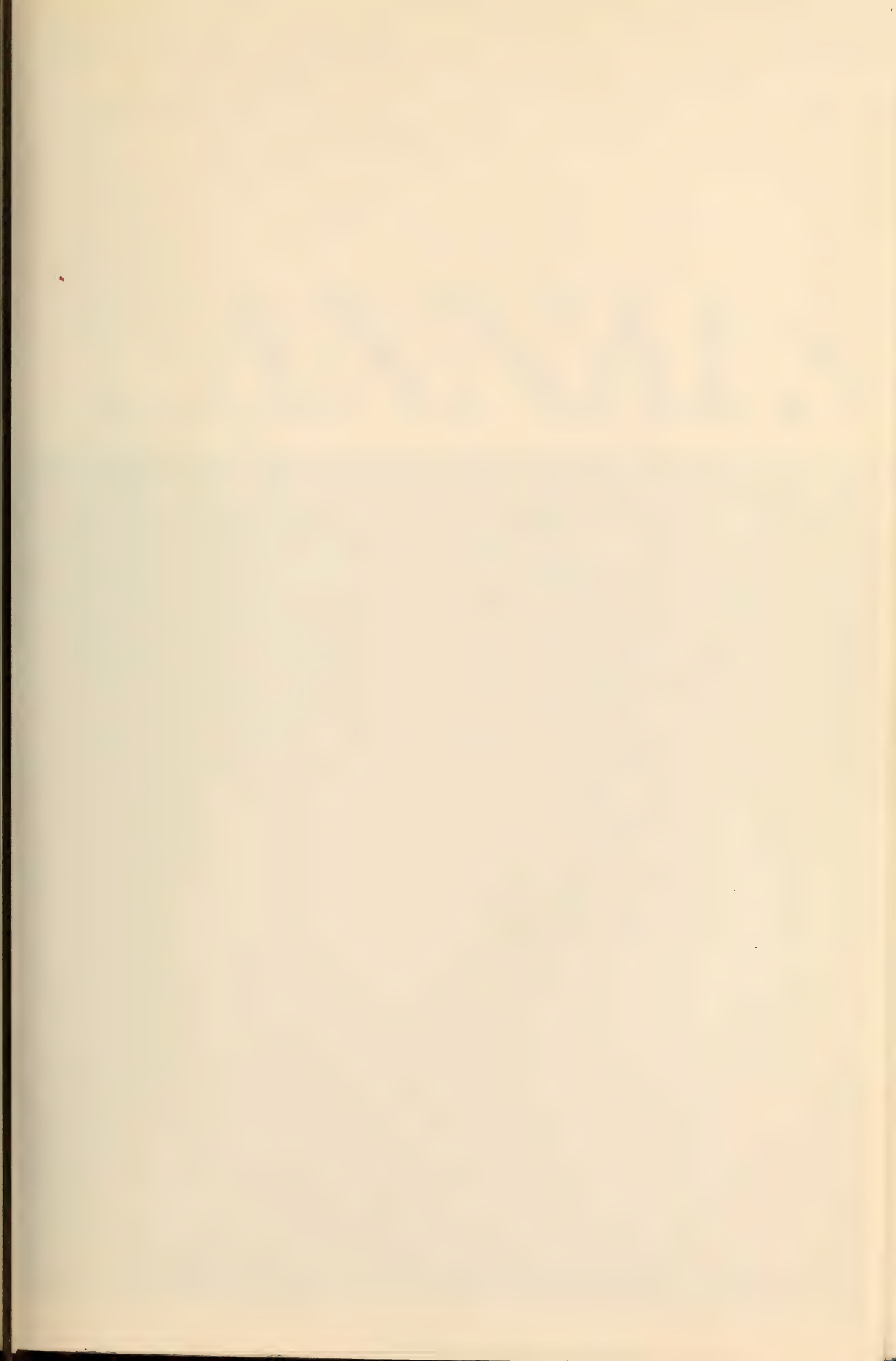
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A. W. Gentry

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BOSELAPHINE (BOVIDAE, MAMMALIA)
FROM SOUTH AFRICA

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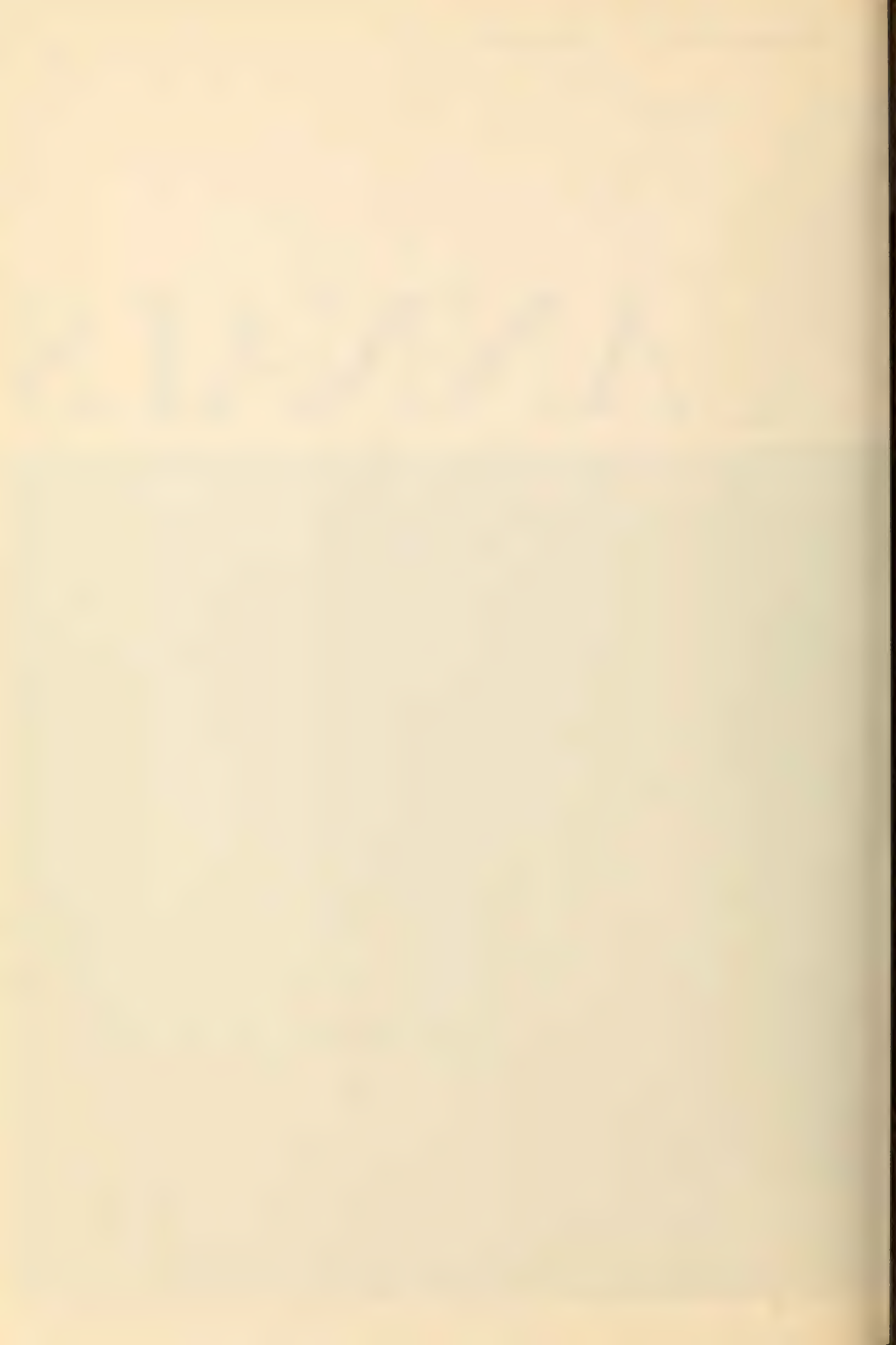
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ORIENTATION AND VARIABILITY IN THE OSSICONES OF AFRICAN SIVATHERIINAE (MAMMALIA : GIRAFFIDAE)

By

JOHN M. HARRIS

P.O. Box 40658, Nairobi, Kenya

(With 5 figures)

[MS. accepted 5 July 1973]

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INTRODUCTION

Singer & Boné (1960) placed most of the Plio-Pleistocene sivatheriines from Africa in the species *Sivatherium olduvaiense*. In addition they recognized *Libytherium maurusium*, founded on a right mandible from Garet Ichkeul, St. Arnaud (Tunisia) and a second species of *Sivatherium*—*S. cingulatum*—based on dental material from South Africa. There seems to be some controversy over the correct identification of the common African sivathere, *Sivatherium olduvaiense* being used by Hopwood (1934) and Singer & Boné (1960) while *Libytherium olduvaiensis* was preferred by Leakey (1965). Arambourg (1960) concluded that *Libytherium maurusium* was conspecific with *Sivatherium olduvaiense*. If Arambourg's interpretation is correct, the genus *Sivatherium* (Falconer & Cautley, 1836) has priority over *Libytherium* (Pomel, 1892) but the species *Sivatherium olduvaiense* is a junior synonym of *Sivatherium maurusium* (Pomel, 1892).

There would, therefore, appear to be two species of *Sivatherium* from Africa—*S. maurusium* and *S. cingulatum*. A third (and the type) species of *Sivatherium*—*S. giganteum*—is known from the Siwalik Series of India.

Sivatherium giganteum has four ossicones (or horns) in the male, an anterior conical pair arising from the frontals and a posterior palmate pair situated on the parietals. The females are believed to lack ossicones. *S. giganteum* thus differs from other genera of Asian sivatheres with ossicones. *Bramatherium* also has four ossicones—two extending upwards from the fronto-parietal region and two extending laterally from the parietals but, in contrast to *Sivatherium*, the anterior ossicones are much larger than the posterior pair. *Hydaspitherium* has one pair of ossicones only, fused at their base into one solid mass, on the fronto-parietal region. *Birgerbohlina*, the only European sivathere, possesses a single

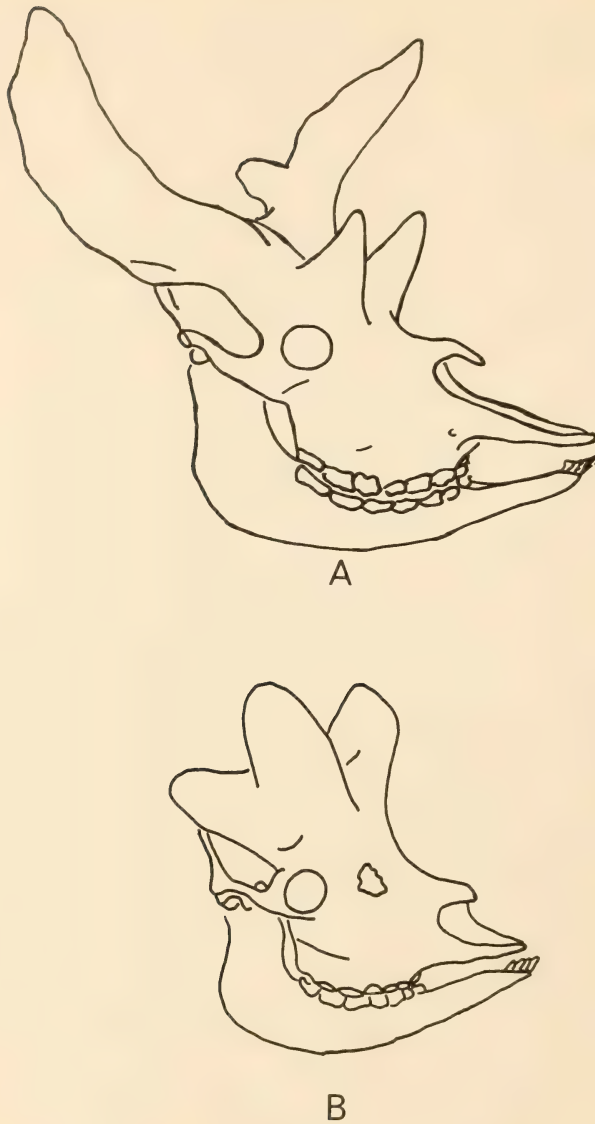


Fig. 1

- A. Skull of *Sivatherium giganteum* (after Colbert 1935).
B. Skull of *Bramatherium* (after Colbert 1935).

pair of ossicones that are aligned vertically and are rounded in cross-section.

Because of the incomplete nature of the African sivatheriine material it has been tempting to orientate the ossicones of the African specimens similarly to those of the Asian *Sivatherium giganteum*. The discovery at East Rudolf, Kenya,

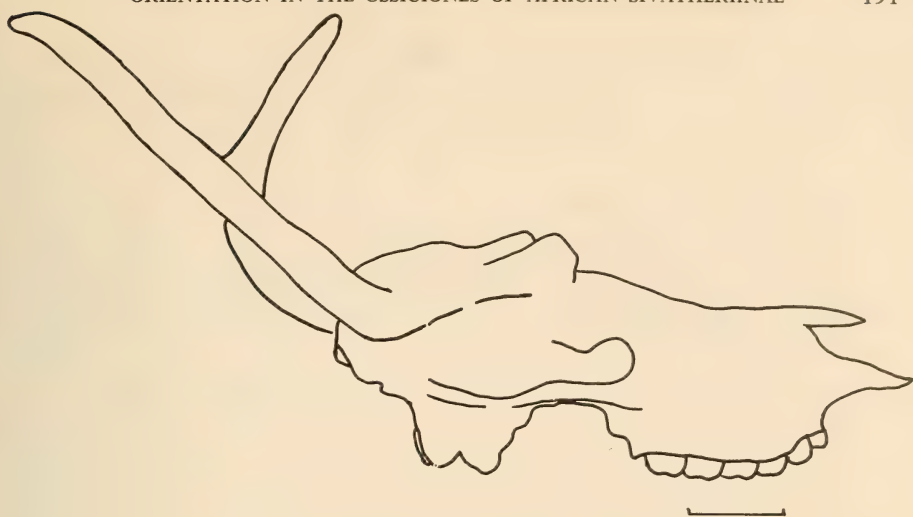


Fig. 2
Sivatherium skull from East Rudolf, Kenya. Scale = 10 cm.

of a virtually complete cranium of *Sivatherium* (Harris in press) has proved of great importance for reinterpreting incomplete ossicones found at other Plio-Pleistocene sites in Africa (Arambourg 1948, 1949; Singer & Boné 1960). The posterior ossicones of the East Rudolf skull are orientated in an entirely different direction from those of *S. giganteum*. Re-examination of ossicones from Olduvai Gorge, Tanzania, has shown that some of the more complete specimens were orientated in accordance with the East Rudolf skull and it is likely that other specimens must be similarly aligned. Some doubt is also thrown on whether the anterior ossicones of the African sivatheriines are in fact separate entities from the posterior ossicones.

POSTERIOR OSSICONES

Two of the Olduvai *Sivatherium* ossicones (Old.1.53 of Singer & Boné (1960) and FLKS 1) extend proximally to include parts of the nuchal crest and may therefore be confidently orientated in light of the East Rudolf skull. Together, these three specimens provide a basis for orientation of other, less complete ossicones. Four factors appear to be of use in orientation—tuberosities, grooves, torsion and cross-section shape.

Tuberosities

Although the posterior ossicones of the African sivatheriines appear to be markedly less palmate than *S. giganteum*, they are ornamented by a flange or flanges and a number of discrete knobs. This ornamentation occurs on the anterior (or distally and, where affected by extreme torsion, lateral) surface of

the ossicone. Discrete knobs have been observed diametrically opposite to the proximal flange in the proximal part of the ossicone but are smaller and fewer in number than on the anterior surface; distally the knobs appear to be confined to one edge.

Grooves

Longitudinal or oblique grooves are often present on the ventral surface of the ossicones. Such grooves differ markedly in development; on some specimens they are very faint, in others they are present on the dorsal surface also. Where grooves are present on both surfaces the dorsal grooves are always distinctly fainter and less numerous than those on the ventral surface.

Cross-section

The ventral surface of the ossicone is normally distinctly more convex than the dorsal surface, especially in the proximal portion.

Torsion

Some sivatheriine ossicones are almost straight, but, where present, torsion is always clockwise from the base outwards on the right ossicone and anti-clockwise on the left (cf. Singer & Boné 1960: 494).

Even on incomplete ossicones a combination of the above features normally serves to orientate the specimen correctly. In view of the above, the following corrections are necessary to plates illustrating Singer & Boné's (1960) monograph:

<i>Plate</i>	<i>Specimen</i>	<i>Side</i>	<i>Stated View</i>	<i>Corrected View</i>
1a	Old.2.53	right	anteromedial	ventral
1b	Old.86	left	anteromedial	lateral
1c	Old.1.53	left	anteromedial	anteroventral
1d	Old.2.53	right	posterolateral	dorsoposterior
1e	Old.1.53	left	posterolateral	posterior
1f	Old.86	left	posterolateral	dorsal
2a	Old.3.53	right	posterolateral	dorsal
2b	Old.3.53	right	anteromedial	ventral
2c	Old.3.53	right	anterior	lateral
3a	M.14955	right	posterodorsal	dorsal
3b	M.14955	right	anteromedial	ventral
3c	Old.52 SHK/BKII + M.14594b	right	anteromedial	ventral
3d	Old.52 SHK/BKII + M.14594b	right	posterolateral	dorsal
29c	C.431A	right	anterior	anterior
29d	C.431A	right	anteromedial	ventral
43a	Hopefield 4372	right	posterolateral	dorsal
43b	Hopefield 4372	right	anterior	anterior
43c	Hopefield 4372	right	anteromedial	ventral
44a	Hopefield 4373	left	anteromedial	ventral
44b	Hopefield 4373	left	anterior	anterior
44c	Hopefield 4373	left	posterolateral	dorsal
51a	St Arnaud, Algeria 1948-1-2	right	anteromedial	anteroventral
51b	St Arnaud, Algeria 1948-1-1	right	medial	dorsal

Once correct orientation has been achieved, three major shapes are apparent in the posterior ossicones of the specimens from Olduvai and appear to be typical of ossicones from other African sites also.

Type A

The posterior ossicone extends outwards and backwards, then perhaps slightly upwards. Flanges and knobs are present on the anterior and lateral surfaces. Torsion is only slight (Fig. 3).

Olduvai examples: FLK S 1, Old.63 BK II 431, Old.5.53, M.14955, M.14954b.

Type B

The ossicone extends outwards, then upwards, then inwards and forwards. The distal tip of the ossicone is thus bent forward and sited in front of the anterior flanges on the proximal portion of the ossicone. Flanges and knobs are sited on the anterior (and, through torsion, outer) edge of the ossicone, but a knob is also present on the posteroventral edge (diametrically opposite to the proximal flange) in the proximal portion of the ossicone (Fig. 4).

Olduvai examples: BK II 068/5746 (= Old.1.53), BK II 068/5747 (= Old.2.53), BK II 068/5753.

Type C

Recognizable parts of the cranium have not been observed attached to ossicones of this type. These ossicones are straight and, it is believed, point directly backwards. Knobs may be present on both medial and lateral edges but are more abundant (and more prominent) on the lateral edges (Fig. 5).

Olduvai examples: Old.68 BK II S.34, Old.53 BK II 86.

Singer & Boné (1960: 494) commented on the variability of the posterior ossicones from Olduvai and suggested that the ossicones exhibiting extreme torsion might possibly represent male specimens. Colbert (1935: 342) agreed with earlier workers that *Sivatherium giganteum* lacked ossicones in the female. It is likely that this also applied to other species of *Sivatherium* and, if this view is correct, all African sivatheriine ossicones are from male animals. Disparity in size and development of the knobs and flanges may represent individual variation, but it is also possible that the amount of secondary bone apposition, in the form of ornamentation, might be a function of the age of the individual.

All the *Sivatherium* posterior ossicones so far collected from Olduvai fall into one of the three morphological groups listed above. It may be that these three groups possess taxonomic significance and certainly the two pairs of associated left and right ossicones (Old.1.53+Old.2.53 and FLK S 1) are symmetrical. Of the two posterior ossicones on the East Rudolf skull, however, the right ossicone falls into Group A and the left into Group B. Material collected from Olduvai subsequent to the publication of Singer & Boné's monograph includes a large number of sivatheriine postcranial elements. These are currently being investigated and it will be interesting to see whether the presence of more than one species of *Sivatherium* is indicated.

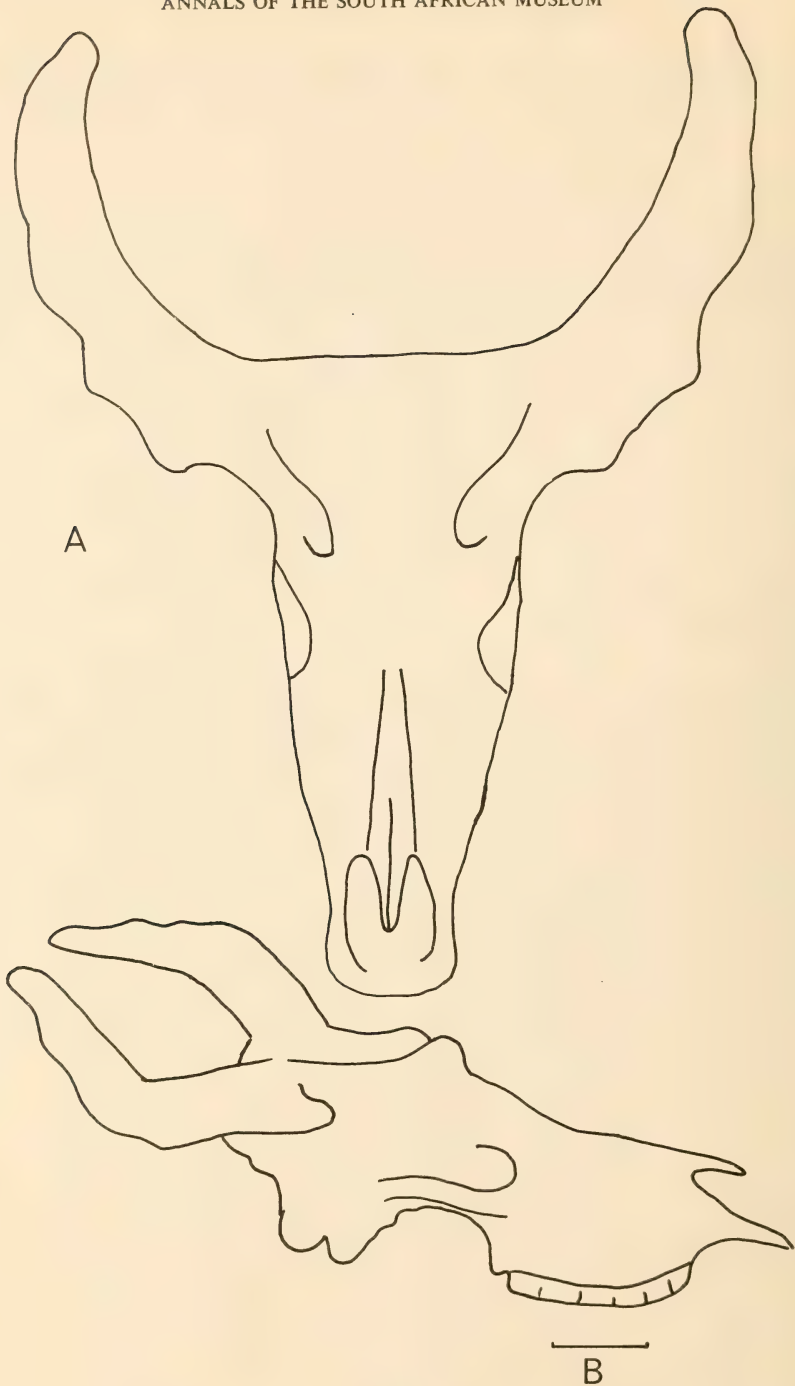


Fig. 3
Restoration of skull of *Sivatherium maurusium* Type A.
A. Dorsal view. B. Lateral view. Scale = 10 cm.

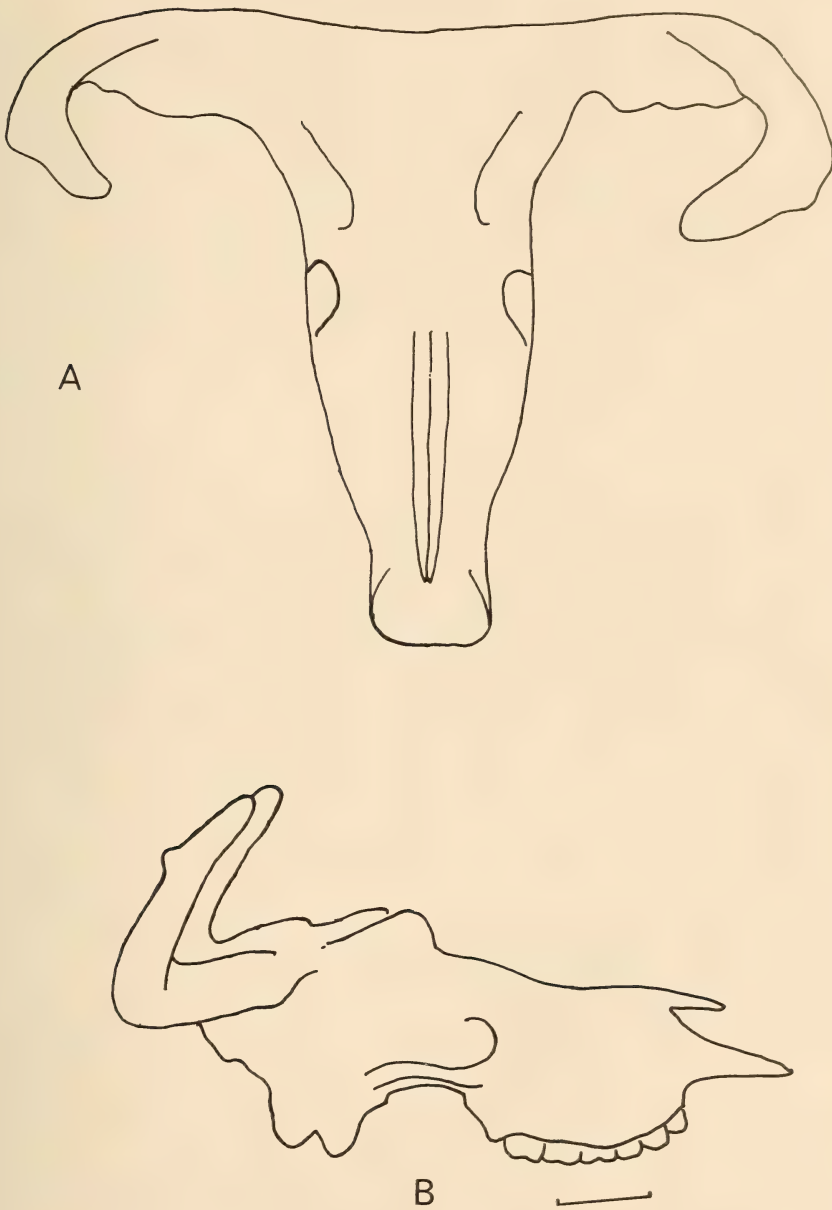


Fig. 4
Restoration of skull of *Sivatherium maurusium* Type B.
A. Dorsal view. B. Lateral view. Scale = 10 cm.

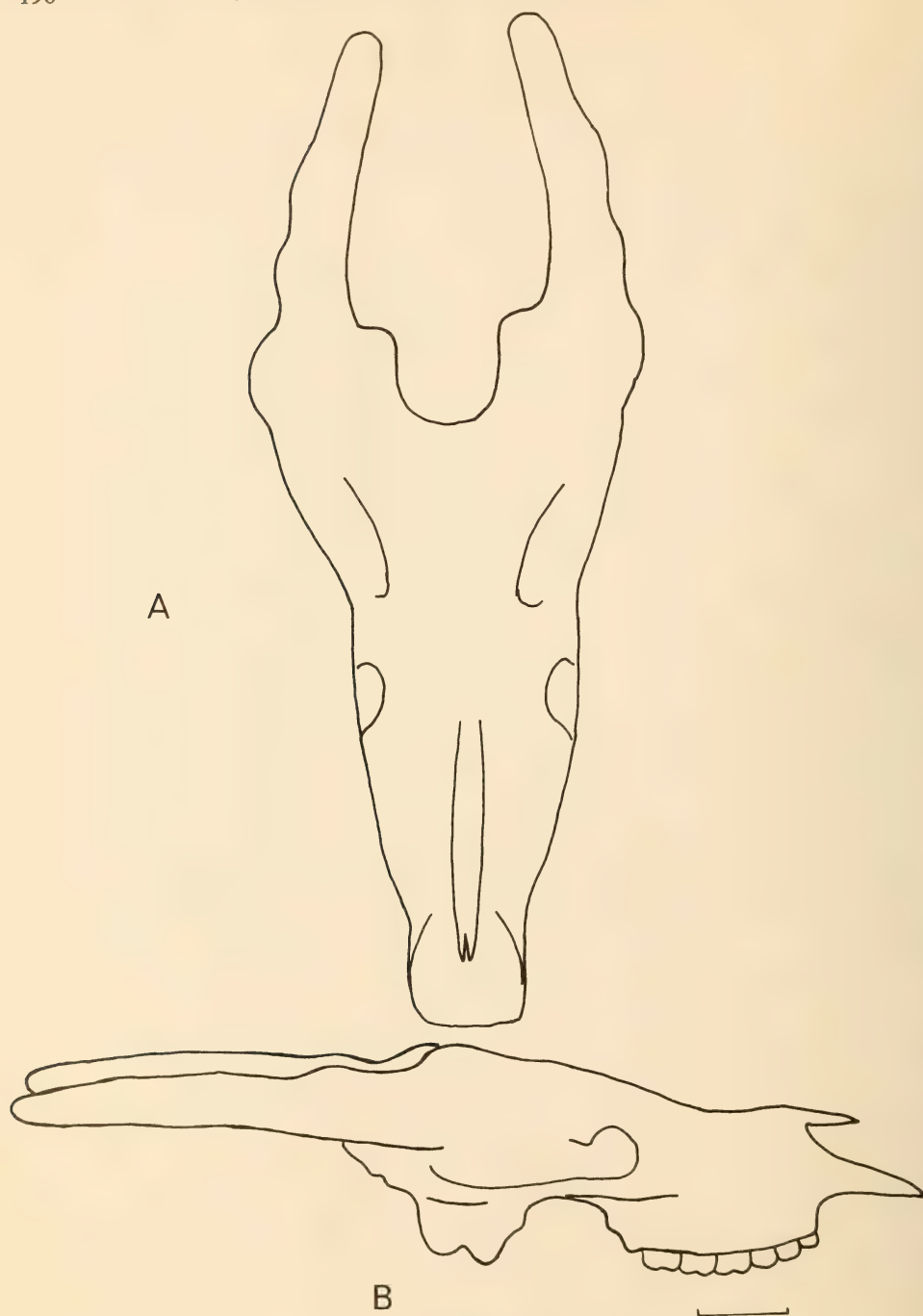


Fig. 5

Restoration of skull of *Sivatherium maurusium* Type C.
A. Dorsal view. B. Lateral view. Scale = 10 cm.

ANTERIOR OSSICONES

Singer & Boné (1960: 492) described anterior ossicones of *Sivatherium maurusium* from Hopefield and Tierfontein. Anterior ossicones are present on the East Rudolf skull and on two Olduvai specimens (Old.68 BK II S.34 and FLK S 1). Anterior ossicones in *Sivatherium giganteum* are discrete forward-projecting conical structures sited above the orbits. Those of the East African specimens appear to be flange-like ossifications sited on the lateral edges of the cranial vaults behind the orbits. There is some doubt whether the 'anterior ossicones' of the East African sivatheriines can be interpreted as discrete structures or merely represent an anterior extension, or the beginning, of the posterior ossicones. None of the East African 'anterior ossicones' are sculpted on one side by the grooves that are present in the Tierfontein specimen (C.431B) and, as such grooves are typical of the posterior ossicones, there must be some doubt about the correct identification of the Hopefield fragment.

DISCUSSION

Quite apart from the distinct possibility of further taxonomic subdivision on the basis of ossicone morphology and postcranial elements, some doubt must also be placed on the current identification to generic level of the African Plio-Pleistocene sivatheriines. As is recorded elsewhere (Harris in press), the skull of *Sivatherium giganteum* has a much shorter facial region and a deeper and wider cranial region than the East Rudolf skull. The posterior ossicones of the African sivatheriines are orientated differently and the anterior ossicones, if interpreted as such, are sited more posteriorly and are less prominently developed. The teeth of the African and Asian sivatheriines are, however, similar in morphology.

It is possible that *Sivatherium maurusium* and *S. cingulatum* may be only specifically distinct from *S. giganteum*. It is also possible that, because the Asian sivatheriine genera overlap considerably in morphology except for their ossicones (Singer & Boné 1960: 520), the different skull shape and ossicone orientation of the African specimens may warrant generic distinction from their Asian relatives. Such major taxonomic realignment must, however, await the results of current investigations into the postcranial anatomy of the African sivatheriines, revision of the Asian forms, and, if possible, retrieval of further specimens from African sites.

SUMMARY

Isolated ossicones of *Sivatherium maurusium* can be orientated by means of their ornamentation, torsion and cross-section. Three basic shapes of posterior ossicone have been observed. The presence of a well-developed anterior ossicone in this taxon is doubtful.

ACKNOWLEDGEMENTS

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IN SOUTHERN AFRICA
(MOLLUSCA, BIVALVIA, HIATELLIDAE)

By
BRIAN KENSLEY

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South African Museum, Cape Town

(With 8 figures and 1 map)

[Ms. accepted 7 August 1973]

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INTRODUCTION

The bivalve genus *Panopea* is represented by about 10 living species in temperate to subtropical seas. All are inhabitants of sand or mud, being buried to depths of 1–2 metres below the substrate surface, in water depths varying from the Low Water of Springs level, to deeper water. The live animal communicates with the overlying water by means of elongate siphons. The North American representative, *P. generosa* Gould, occurs in large numbers in the region of Puget Sound, where, under the name ‘geoduck’, the living animals are eagerly sought after as culinary delicacies (Phillips 1970). Elsewhere, other species are apparently not as common.

As a fossil form, the genus is known from Lower Cretaceous to Recent times, and is represented by numerous species. In South Africa, *P. gurgitis* (Brongniart) is known from the Lower Cretaceous (Neocomian) of Uitenhage and Zululand.

Regarding younger forms from South Africa, Stow (1871), reporting on a raised beach in the Port Elizabeth district, mentioned the presence of a fossil *Panopea*. Earlier, in 1855, Woodward proposed the name *P. natalensis* for a specimen erroneously recorded from Natal but in fact coming from Angola. Since then several more specimens have been recorded from various sites, under a variety of names. Woodward (1855) mentioned the similarity of *P. natalensis* to

the Mediterranean *P. aldrovandi*, while Barnard (1964: 559), using the name *P. aldrovandi* for Pleistocene forms, raised the following question: 'Are there any clear-cut characters apart from minor and inconstant differences in shape due to growth changes, which will serve to differentiate these so-called species?'

Since more Pleistocene specimens have become available, it was thought necessary to establish the systematic position of this species beyond any reasonable doubt. With this in view, the present investigation was carried out. Specimens, both fossil and recent, were obtained from as many sources as possible (Table 1).

It must be noted that the exact age of many of the South African 'beach' deposits, referred to either as early Pleistocene or late Tertiary, is still uncertainly determined, and that the term 'Plio-Pleistocene' is deliberately used in the present work in its broadest sense.

SYSTEMATIC DISCUSSION

Phylum MOLLUSCA

Class BIVALVIA

Order MYOIDA

Family Hiatellidae

Genus *Panopea* Ménard de la Groye, 1807

Apart from the characteristics of the family, the genus *Panopea* is characterized by the possession of a large ligamental nymph, a wide pallial sinus, and valves gaping at both ends.

Subgenus *Panopea*

The subgenus *Panopea* is characterized by a continuous pallial line, and a single cardinal tooth in each valve.

Panopea (Panopea) glycymeris (Born)

SYNONYMY

Mya glycymeris was the name first used in a valid description of the present species and is given first in the synonymy.

Panopea aldrovandi Ménard, 1807, was the first usage of the valid generic name for the present species (*Mya* and *Glycymeris* both having been pre-occupied), and is given next in the synonymy. This is followed by the correct designation, i.e. *Panopea glycymeris*. As a proliferation of names has been used with reference to the present species, the rest of the synonymy has been given alphabetically, with entries under each name listed chronologically.

Mya glycymeris Born, 1778: 10; 1780: 20. Chemnitz, 1782: 33. Gmelin, 1790: 3222. Montagu, 1808: 19. Turton, 1819: 107. Wood, 1825: 13.



Fig. 1. *Panopea glycymeris*: External view.

a. Sicily; b. Portugal; c. Moçâmedes; d. Baía dos Tigres; e. Velddrif; f. Klein Brak River.

Panopea aldrovandi, Ménard, 1807: 136; 1808: 464. Nicklès, 1950: 228. Franca 1960: 37. Barnard, 1964: 557.

Panopea glycymeris: Lamy, 1925: 267. Thiele, 1935: 924. Imperatori, 1961: 141. Ghisotti & Steinmann, 1969: Sheet 78-Ac-01. Treatise, 1969: N700.

Glycymeris aldrovandi: Pally, 1900: 410; 1920: 94.

Glycymeris glycymeris: Gray, 1847: 189. Tryon, 1869: 60. Malatesta & Nicosia, 1955: 177.

Glycymeris rugosa: Bosc, 1802: 5. Adams & Adams, 1856: 350.

Glycymeris aldrovandi: Fischer, 1880-1887: 1125.

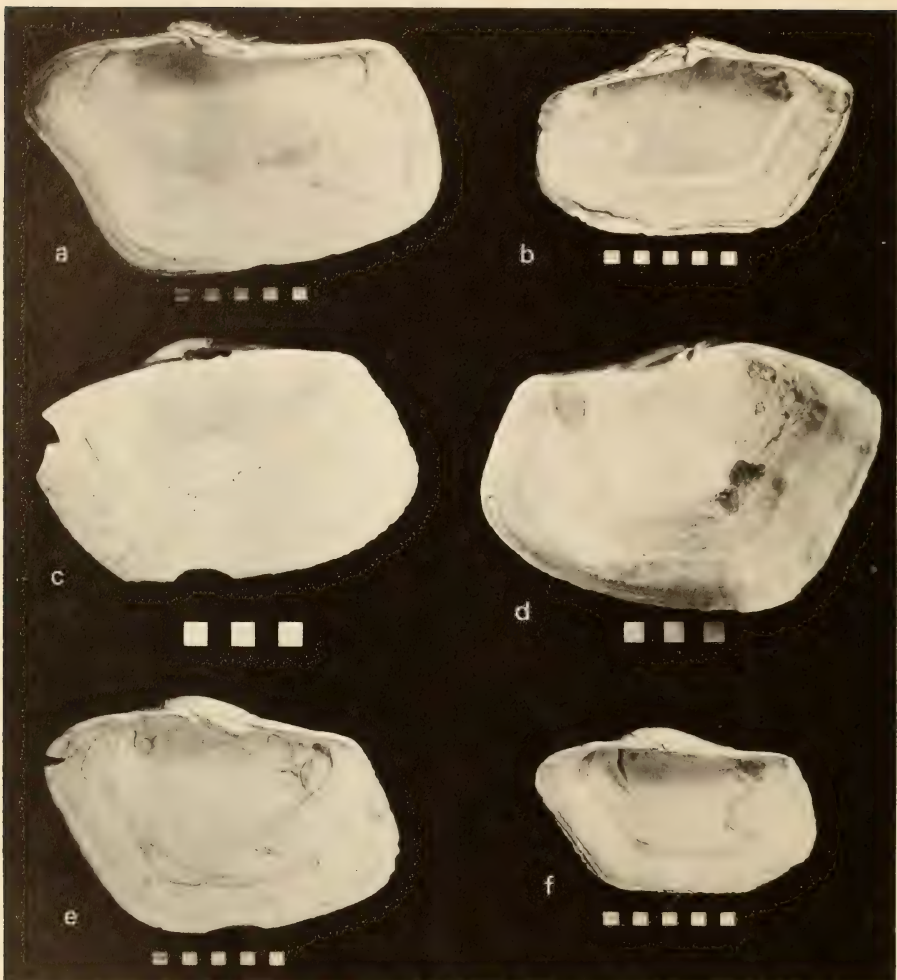


Fig. 2. *Panopea glycymeris*: Internal view.

a. Sicily; b. Portugal; c. Moçâmedes; d. Baía dos Tigres; e. Velddrif; f. Klein Brak River.

Panopae aldrovandi: Lamarck, 1818: 457.

Panopaea aldrovandi: Blainville, 1825-27: 571. Deshayes, 1832: 698; 1835: 67. Philippi, 1836-44: 6, 7. Valenciennes, 1839: pl. 1. Deshayes, 1843: 133. Potiez & Michaud, 1844: 259. Forbes & Hanley, 1853: 178. Woodward, 1855: 218. Sowerby, 1873: pl. 1. Debeaux, 1884: 510. Clessin, 1895: 46. Dautzenberg, 1910: 148; 1912: 99.

Panopaea attenuata Sowerby, 1893: pl. 3; 1889: 156. Clessin, 1895: 45.

Panopaea australis Valenciennes, (*non* Sowerby), 1839: 3, 34; 1843: pl. 8, pl. 12. Woodward (*non* Sowerby), 1855: 220.

- Panopaea cyclopana* Di Monterosato, 1889: 26. Locard, 1892: 256.
- Panopaea faujasii*: Philippi, 1836-44: 6, 7. Valenciennes, 1843: pls. 2, 3, 4, 6. Wood, 1853: 283. Chenu, 1862: 27. Sowerby, 1873: pl 2. Clessin, 1895: 51.
- Panopaea glycimeria*: Locard, 1886: 384.
- Panopaea glycimeris*: Brown, 1827: pl. 10. Deshayes, 1843: 5. Brown, 1844: 112. Petit de la Saussaye, 1869: 33. Mayer, 1870: 24, 39. Di Monterosato, 1875: 19; 1878: 75. Crosse, 1884: 191. Petersen, 1888: 159. Moncharmont Zei, 1960: 184. Di Monterosato, 1889: 26. Nobre, 1938-40: 712. Ruggieri, 1943-44: 99; 1948: 70; 1949: 92.
- Panopaea glycymeris*: Turton, 1822: 42. Brown, 1827: pl. 10. De Gregorio, 1929: 5. Ekman, 1953: 84. Priolo, 1966: 669.
- Panopaea glycymeris faujasi*: Chiesa, 1932: 171.
- Panopaea natalensis*: Woodward, 1855: 220. Smith, 1906: 294. Schwarz, 1910: 115. Barnard, 1951: 167.
- Panopea dreyeri* Van Hoepen, 1940: 186.
- Panopea glycimeris*: Winckworth & Winckworth, 1935: 162. De Stefani, 1941: 274.
- Panopea glycymeris* var. *rugosa* Lamy, 1925: 269.
- Panopea natalensis* Woodward, 1855: 220. Smith, 1903: 399. Lamy, 1925: 271. Barnard, 1962: 187.
- Panope faujasii* Ménard, 1807: 115.

MATERIAL AND MEASUREMENTS

A complete list of the material examined is given in Table 1. Only shell characters were used for comparative purposes. These characters include hinge structure, muscle and pallial scars, and general proportions. For the comparison of general proportions, the following measurements were used:

- greatest diagonal length (a)
- umbo to ventral margin (b)
- umbo to antero-dorsal corner (c)
- umbo to postero-ventral corner (d)

Figure 3 illustrates these dimensions, which were taken for all measurable specimens. In the case where both valves of the shell are preserved, only one valve was measured. Figure 5 illustrates the scatter resulting from the plotting of diagonal length against the distance from the umbo to the ventral margin. Figure 6 illustrates the scatter obtained from a comparison of the distance from the umbo to the antero-dorsal corner with the distance from the umbo to the postero-ventral corner. (Because of the very gradual curve of the postero-dorsal margin, umbo to postero-dorsal corner is difficult to measure, and was not used.)

Table 1

Specimen	Locality	Valves	Greatest diagonal length mm	Umbo to ventral margin mm	Umbo to antero-dorsal corner mm	Umbo to postero-ventral corner mm
Paris Museum	Mediterranean	L & R	247	127	105	170
Paris Museum	Sicily	L & R	272	146	114	189
Paris Museum	Portugal	L	211	120	104	131
British Museum	Malta	L & R	246	132	106	170
S.A. Museum	Mediterranean	R	173	88	71	115
Lisbon	Baia dos Tigres	L	204	126	96	121
Lisbon	Moçâmedes	R	167	92	72	112
Geological Survey	Velddrif	R	240	132	112	154
S.A. Museum						
K4391	Velddrif	L & R	234	133	95	159
K4390	Velddrif	L & R	244	133	112	158
K4393	Velddrif	L & R	202	109	87	137
K4394	Velddrif	L & R	198	114	88	129
K4395	Velddrif	L & R	228	131	100	155
A2139	Velddrif	L & R	209	111	82	150
Geological Survey	Klein Brak River	L & R	185	95	84	121
National Museum						
D2010a	Klein Brak River	R	205	116	83	143
D2010b	Klein Brak River	R	194	103	84	128
D2010c	Klein Brak River	L	178	95	75	117
D2010d	Klein Brak River	R	183	99	74	125
D2010e	Klein Brak River	L	155	84	61	104
D2010f	Klein Brak River	L	162	92	71	113
D2010g	Klein Brak River	R	209	104	90	133
S.A. Museum						
K4385	Klein Brak River	L & R	183	99	77	122
K4389	Klein Brak River	L & R	165	93	71	112
K4384	Klein Brak River	L & R	180	98	71	125
K4383	Klein Brak River	L	197	118	83	134
K4386	Klein Brak River	L & R	168	83	65	115
K4388	Klein Brak River	L	184	103	76	132
3486	Klein Brak River	L & R	157	91	68	119

The following material, being damaged, could not be measured:

S.A. Museum. Velddrif L & R, L, R
 Geological Survey. Velddrif 2 fragments
 Paris Museum. Dakar L

The possibility was considered that shell proportions changed differently with growth in the different populations. With this in mind, 2 individuals were selected from each of the Mediterranean, Velddrif and Klein Brak populations, and 6 growth lines traced on each of these. The length/height ratios were plotted for each of these growth lines and are shown in Figure 7. These dimensions are given in Table 2. In each case, the final length/height set represents the total dimensions of the specimen. For convenience, height was measured, not from the umbo, but from the most dorsal point of the shell as illustrated in Figure 4.

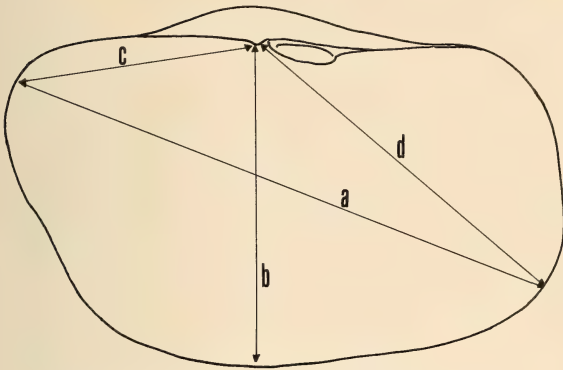


Fig. 3. Diagram to illustrate dimensions used.

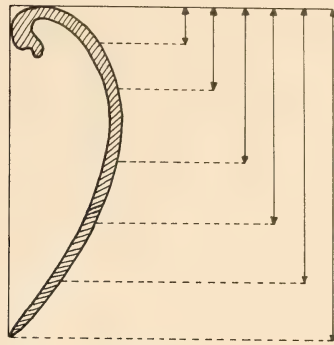


Fig. 4. Diagram to illustrate method of growth-line measurement.

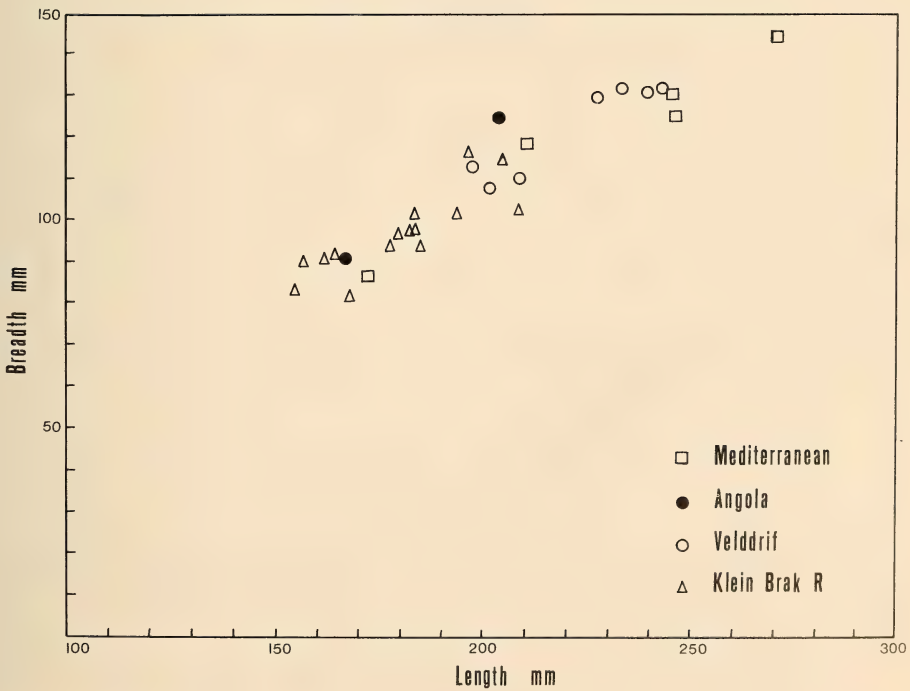


Fig. 5

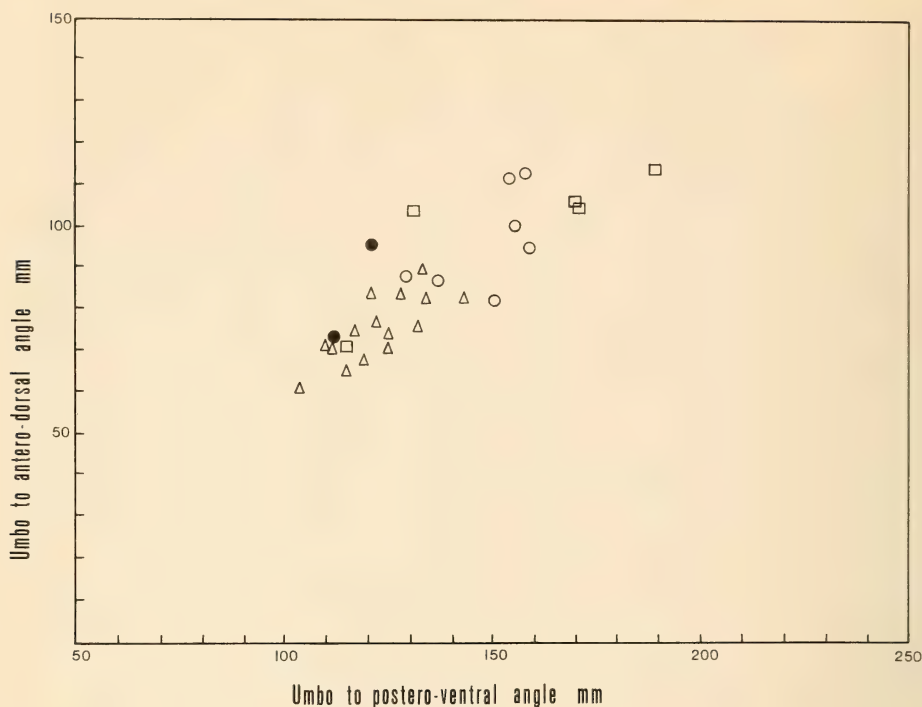


Fig. 6

Table 2

Specimen	Locality	Growth-line Measurements: Length \times Height mm					
Paris Museum	Sicily	48 \times 31	102 \times 65	165 \times 100	197 \times 118	236 \times 145	272 \times 159
British Museum	Malta	24 \times 16	78 \times 46	113 \times 75	177 \times 109	200 \times 122	246 \times 144
Geological Survey	Klein Brak River	41 \times 25	75 \times 46	109 \times 64	141 \times 84	170 \times 93	185 \times 103
S.A. Museum							
K4385	Klein Brak River	27 \times 16	59 \times 38	95 \times 58	147 \times 88	167 \times 98	183 \times 102
K4391	Velddrif	52 \times 31	109 \times 66	147 \times 87	182 \times 109	210 \times 128	234 \times 145
K4390	Velddrif	56 \times 34	88 \times 58	121 \times 76	189 \times 114	213 \times 135	244 \times 145

SOUTHERN AFRICAN LOCALITIES (See map)

Zwartkops, Port Elizabeth

Originally designated as Pliocene or Post-Pliocene (Stow 1871) it has been suggested that these formations are of Pleistocene age (Schwarz 1910).

Klein Brak River, Mossel Bay (Rogers 1906; Schwarz 1910)

These deposits have a similar age to the previous locality, i.e. Plio-Pleistocene.

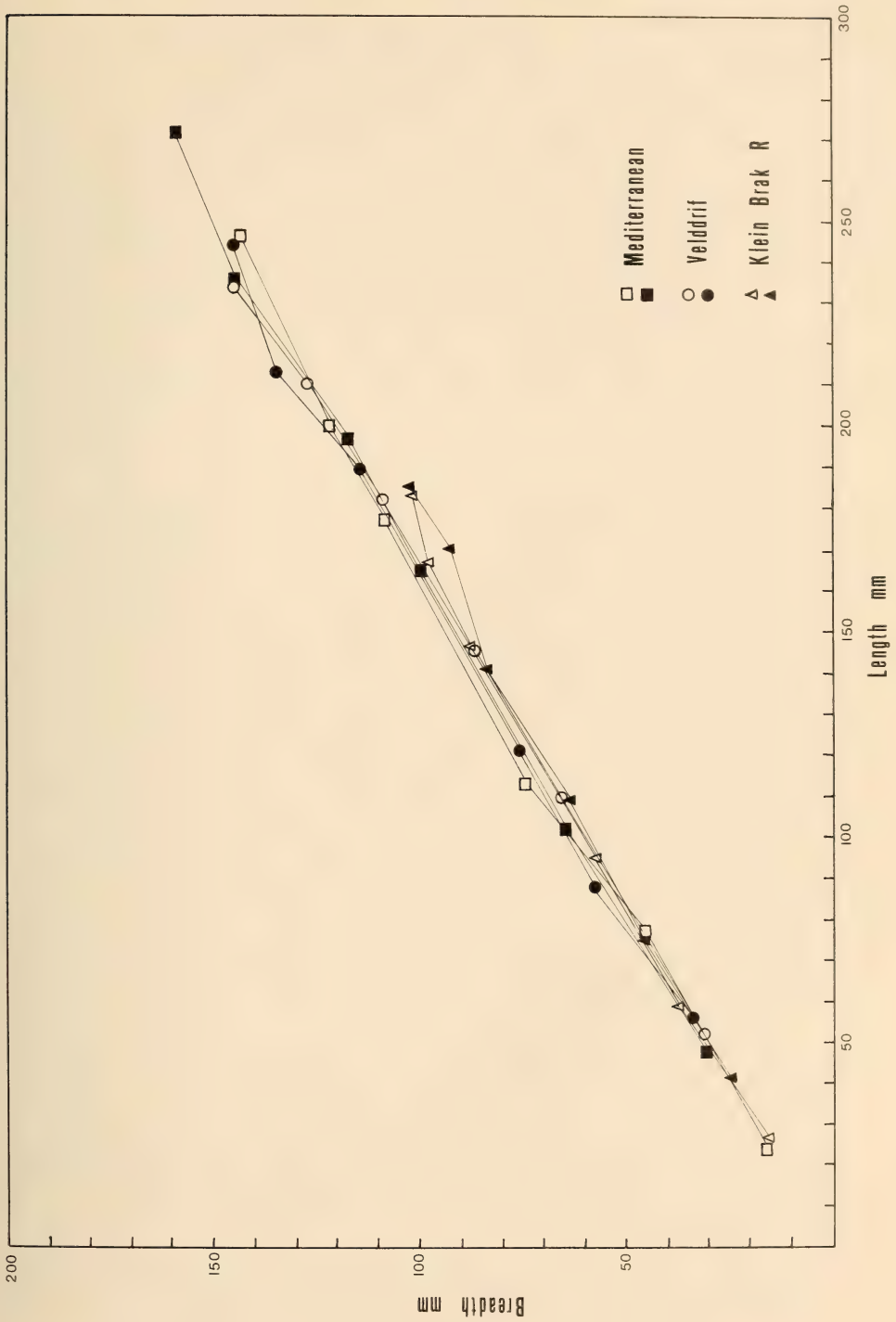
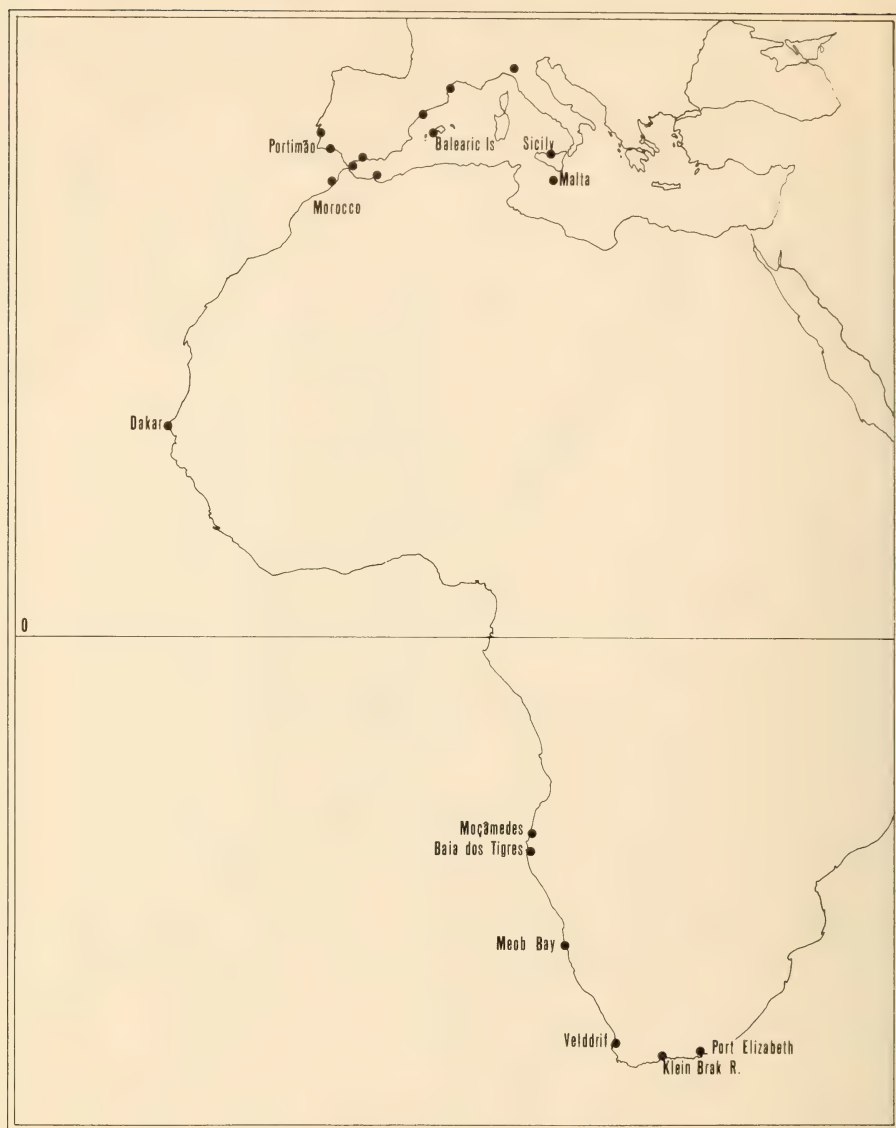


Fig. 7



MAP 1. Locality map for *Panopea glycymeris*.

Velddrif

Situated near the mouth of the Great Berg River, the farm 'Kruispad', 8 km from the present seashore on the west coast, has been given a Pleistocene age (Visser & Schoch 1973).

Meob Bay, South West Africa

The exact origin of these specimens is uncertain, as they were washed ashore at springtide.

Baia dos Tigres, Angola (Franca 1960)

Whether this specimen is from a recently living animal, or a fossil from a raised beach deposit, is difficult to establish. In appearance, state of preservation, it is not unlike some of the material from Klein Brak River.

Moçâmedes, Angola (Franca 1960)

This is a valve from a recently living animal, as a portion of the external ligament is preserved.

MEDITERRANEAN AND WEST AFRICAN LOCALITIES

Atlantic coasts of Portugal and Spain; Mediterranean coasts of Spain, France, Italy, Morocco; Balearic Islands; Sicily; Malta; Port of Dakar, Senegal.

DESCRIPTION

Shell equivalve, elongate, roughly trapezoidal, gaping at both ends, strongly vaulted. Umbo situated slightly anterior to midpoint, just below dorsal vault. Hinge axis and dorsal margin more or less straight. Anterior margin slightly concave, sloping posteriorly in the ventral region. Antero-dorsal corner evenly rounded. Posterior margin truncate, postero-dorsal and postero-ventral corners smoothly rounded. Hinge bearing slight conical protruding cardinal tooth in each valve, situated just below umbo. Tooth of right valve fitting into hollow anterior to cardinal tooth of left valve. Cardinal tooth bearing a fine mid-dorsal ridge. Posterior to tooth, a stout, solid, elongate roughly rectangular structure. Nymph narrow near umbo, widening posteriorly.

Interior of valves with roughly oval anterior adductor muscle scar, posterior broad, irregular, but always continuous. Pallial sinus variable, triangular to rounded. One to several thin lamellar structures sometimes developed in dorsal half of valve, usually running obliquely from internal dorsal margin, alongside adductor muscle scar, more frequently seen in shells from Klein Brak River, function possibly to give added strength to strongly vaulted shell. Margin of shell often eroded, revealing layered structure; occasionally, perhaps due to injury, more extensive layers of calcareous material becomes separated from rest of surface of shell.

Exterior of valves bearing rounded concentric ridges, smoother and more regular at early growth stages. Ridges and growth lines becoming irregular with age. Overall external surface smoothness varying with individuals. Fine short oblique striae sometimes developed in region of ventral margin.

While the material from the Velddrif area is usually bleached white and often fractured, the material from Klein Brak River usually has a remarkably fresh appearance, and could be mistaken for living, were it not that the localities in the raised beaches are so well recorded. In both these localities, specimens with both valves preserved in the 'living' position are sometimes found.

DISCUSSION

Comparison of the hinge lines of specimens from the different localities failed to reveal any differences either in size or disposition of the structures (Fig. 8). (Note: the protruding cardinal tooth tends to be broken off.)

The pallial line and pallial sinus both appeared to be variable between individuals from the same locality and therefore of no diagnostic value. From Figures 5 and 6, it would be difficult to separate any populations; indeed, both figures would seem to indicate a single continuous 'population'. The lines obtained from growth-line measurements (Fig. 7) would seem to indicate that the pattern of growth is similar in the Klein Brak River, Velddrif, and Mediterranean populations, especially during the younger stages. With age, individuals may become distorted and display more irregular growth. It is of interest to note that of the 15 Klein Brak specimens, 209×104 mm is the maximum size attained, whereas five of the six Velddrif specimens, and four of the five Mediterranean specimens exceed these dimensions, the Mediterranean specimens being, on the average, the largest.

The variety *rugosa* mentioned by Lamy (1925) from the Atlantic coast of Portugal and Morocco, would seem merely to be individuals showing a higher degree of rugosity, several of the Klein Brak specimens being equally rugose. The more pronounced roughness may well be due to the inhabiting of a substrate more prone to shifting by greater water movement, as, for example, on the exposed Atlantic coasts.

P. dreyeri, described by Van Hoepen (1940) from the Klein Brak deposits, was separated, as already pointed out by Barnard (1964), on the basis of individual variation.

The Plio-Pleistocene of the Mediterranean has yielded numerous examples of *P. glycymeris*. The fossil form was originally designated as *P. faujasi*, but has long been recognized as being synonymous with the living Mediterranean form (Priolo 1966).

It would seem from the foregoing data, that the same specific name should be applied to the living Mediterranean and West African forms, as well as to the fossils from the Mediterranean, South West Africa and the Cape.

BRIEF ECOLOGICAL OBSERVATIONS

Ekman (1953, 1967), in discussing the fauna of the Mediterranean, regarded *Panopea glycymeris* as an endemic form. The inaccuracy of this statement was hinted at by Barnard (1962, 1964) and is now confirmed. Discussing the hydrography of the Mediterranean, Ekman (1967: 81) states that the south-east Mediterranean in summer has a temperature of $25-27^{\circ}\text{C}$, the rest having a temperature of $20-25^{\circ}\text{C}$. In spite of the fact that winter temperatures drop well below these levels, the area may nevertheless be regarded as warm-temperate.

The port of Dakar, situated on the bulge of Africa, lies within an area where

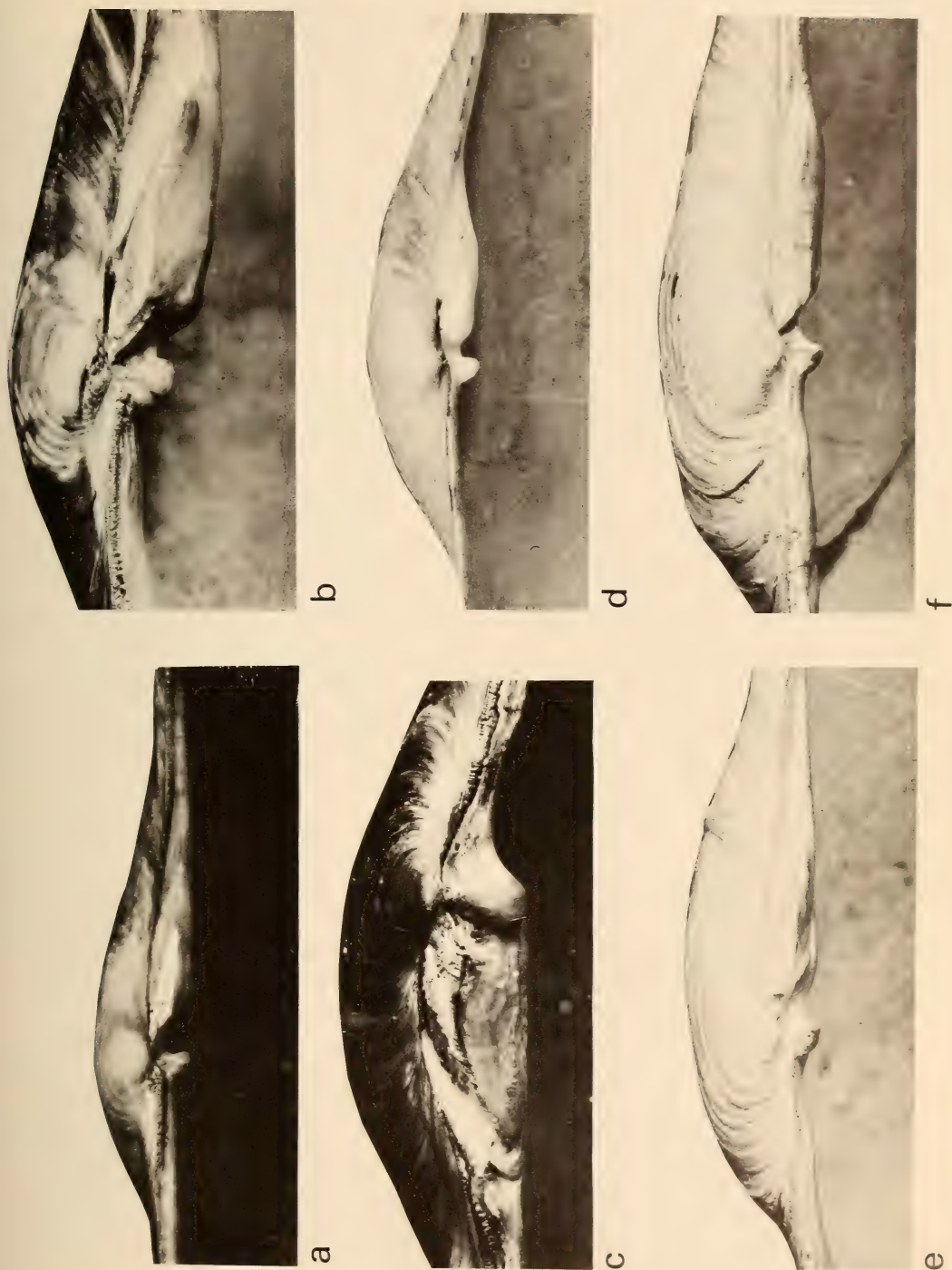


Fig. 8. *Panopea glycymeris*: Hinge lines.
a Mediterranean; b. Sicily; c. Portugal; d. Moçâmedes; e. Velddrif; f. Klein Brak River.

the surface water temperature is usually above 20°C, although at 100 m depth the annual mean temperature is 18° or 19°C (Ekman 1967: 56).

In contrast to the present-day cold-temperate conditions of the sea off the west coast of southern Africa, and the only slightly warmer conditions off the south coast, Plio-Pleistocene conditions must have been rather different. It has been suggested that along both the west and south coasts of South Africa, warmer water than that of the present supported a characteristically warm-water fauna (Carrington & Kensley 1969; Visser & Schoch 1973) during part of the Pleistocene. The presence of *Panopea* in the Plio-Pleistocene deposits is yet another indication of warmer conditions in the past. With the change to the present cold-water regime, *Panopea* apparently died out at the southern end of its range, probably due to the inability of either the juvenile forms or the adults to adapt physiologically to the changed conditions. It is of interest to note that amongst the sediments removed from between valves of *Panopea* from the Velddrif area, valves of the small bivalve *Nuculana bicuspidata* were found. This species, which has also been recorded from the marine terraces of the Cape Cross area, has a present-day distribution from Angola to Mauritania (Nicklès 1950). The sediments from between valves of the Klein Brak deposits yield, amongst a large assortment of molluscs, numerous examples of the small trochid gastropod *Cantharidus fultoni* (now only occurring alive from Moçambique northwards along the East African coast), and a species of the bivalve *Diplodonta* provisionally recorded by Barnard (1962) as *senegalensis*, but which would appear to be very similar to *D. diaphana*, recorded from the Quaternary of Benguela, Angola, and living from Angola to Mauritania. These isolated examples would all seem to point to the existence of warmer water conditions along the west and south coast of South Africa during the Pleistocene.

SUMMARY

The Plio-Pleistocene specimens of *Panopea* from South Africa are compared with shells of living material from the Mediterranean and West Africa. As no differences between the various specimens could be found, it is decided that all belong to the same species, viz. *Panopea (Panopea) glycymeris* (Born).

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(MOLLUSCA, BIVALVIA, HIATELLIDAE)

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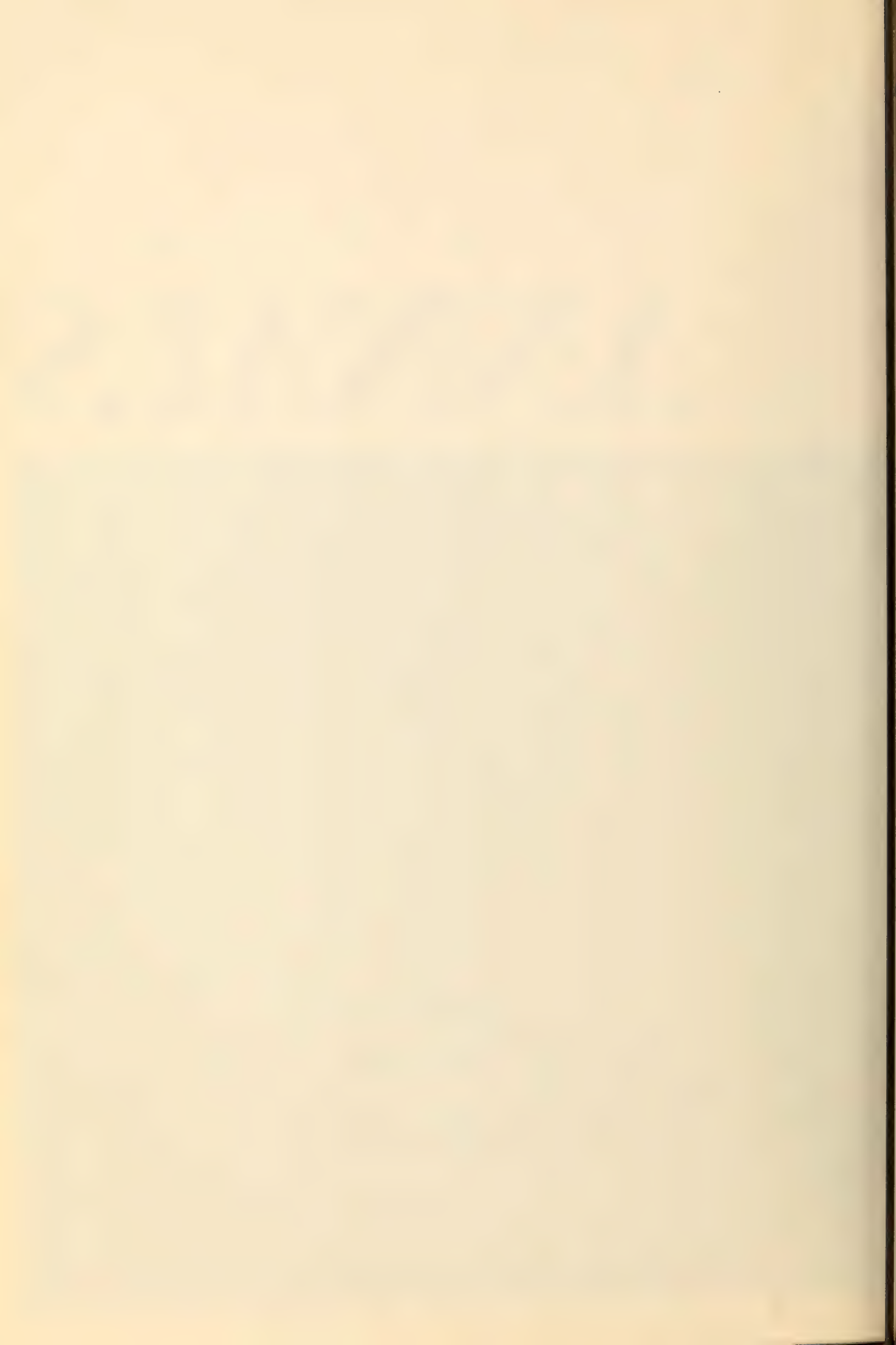
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PETROLOGY AND ORIGIN OF THE PHOSPHORITE
AND ALUMINIUM PHOSPHATE ROCK OF THE
LANGEBAANWEG—SALDANHA AREA,
SOUTH-WESTERN CAPE PROVINCE

By
ANTHONY J. TANKARD

Cape Town Kaapstad

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ANTHONY J. TANKARD

South African Museum, Cape Town

(With 25 figures and 3 tables)

[Ms. accepted 8 August 1973]

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INTRODUCTION

Phosphorite is the term used to describe marine sedimentary deposits which contain more than 18 per cent P_2O_5 , approximating to 50 per cent apatite (Bushinsky 1966). The apatite, generally a carbonate-fluorapatite (Altschuler *et al.* 1958), forms authigenically in a shallow marine environment, giving rise to phosphate rock and nodules. Reworking of the phosphate rock produces pelletal phosphorite. Since the pelletal phosphorite is a product of erosion of a phosphatic rock it must necessarily be a shallow-water deposit whereas nodules and rock phosphate can be found in considerably deeper water. The present-day occurrence of phosphorite on land may be attributed to both tectonic and eustatic causes.

Although submarine phosphorites were first recorded on the Agulhas Bank by the Challenger Expedition of 1873–6 (Murray & Renard 1891), relatively few studies have been made of South African phosphorites, viz. Haughton (1932), Cayeux (1934), Frankel (1943), Parker (1971), Parker & Siesser (1972), Parker & Simpson (1972), Summerhayes *et al.* (1972), Summerhayes (1973), Tankard (1974). However, a voluminous literature discusses phosphorite deposits from other parts of the world (for example, Sheldon 1964; D'Anglejan 1967; McKelvey 1967; Rooney & Kerr 1967; Tooms *et al.* 1969).

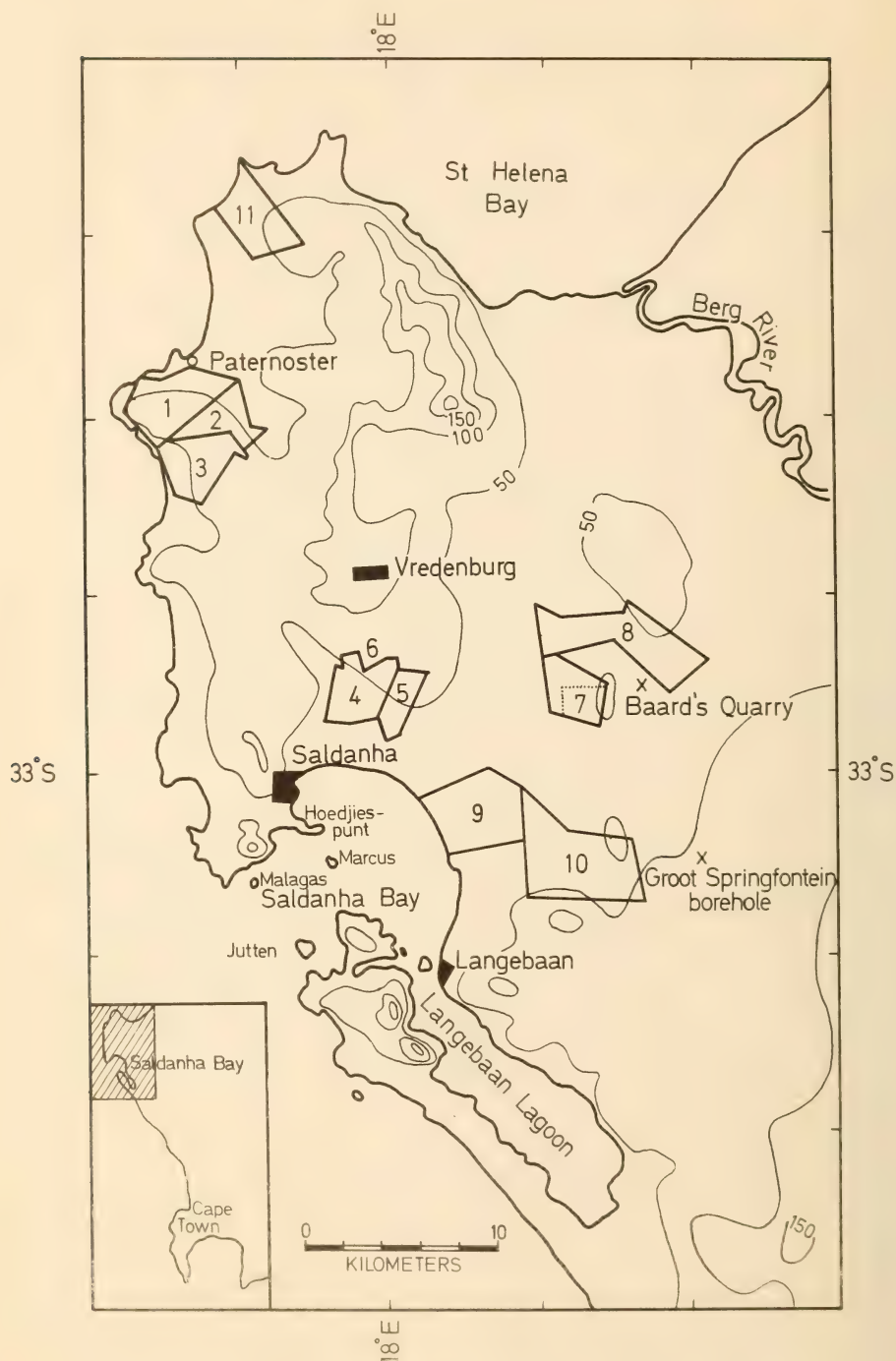


Fig. 1

Locality map of farms prospected. 1, Pelgrimsrus; 2, Noodhulp; 3, Besterskraal; 4, Sandheuwel; 5, Langlaagte; 6, Witteklip; 7, Langeberg; 8, Muishondsfontein; 9, Tiekosklip; 10, Waschkliip; 11, Duyker Eiland.

On the granite hills north and south of Saldanha Bay there are aluminium phosphates which have been discussed by Du Toit (1917), Hutchinson (1950) and Visser & Schoch (1973). They probably originated by leaching of guano deposits by ground water and the subsequent alteration of the granite bedrock to form aluminium and aluminium iron phosphates.

METHODS

All sediment samples were obtained from Chemfos Ltd who used a Selby coring technique, driving a 1,07 m long cylinder into the sediment. The coring was part of their mining and prospecting programme.

Pelletal phosphorite concentrates were obtained by heavy liquid (bromoform) separation from the detrital quartz.

Scanning electron photomicrographs were obtained on the JEOL JSM U3 instrument at Rhodes University. Specimens were coated with a gold-palladium alloy, vacuum evaporated. Coating was done from high and low angles and the samples rotated to obtain an even coating.

GEOLOGIC SETTING

The phosphorite deposits with which this report is concerned are situated primarily about the perimeter of an erosional basin between Langebaanweg and Saldanha (Fig. 1). The areal extent of the Varswater Formation has been established by examination of several hundred logs of boreholes, both within this basin area and on the Atlantic coast between Saldanha Bay and St. Helena Bay. The stratigraphy and lithology of the Varswater Formation and associated sediments are summarized in Table 1. They have been fully discussed elsewhere (Tankard in press).

Lying unconformably below the Varswater Formation on Langeberg is the Middle Miocene basal bed (Tankard in press), a phosphatic sandstone in which the apatite has formed authigenically. This phase of deposition was followed by regression and tilting. In the Pliocene a transgressing sea pushed deltaic marsh sediments ahead of it until it reached a temporary stillstand; the littoral zone is now at 30 m above sea-level. These temporarily stable conditions allowed a barrier bar to build up, behind which estuarine conditions prevailed. The estuary was fed by a river from the north-east. The final transgression reworked the older deposits. The maximum extent of the final transgression is now recorded at 50 to 55 m a.s.l. Erosion of the basal bed during the final transgression supplied the pelletal phosphorite which characterizes the Pelletal Phosphorite Member.

There is little evidence in these sediments of higher than present sea-levels during the Pleistocene. The Pleistocene is represented only by sheets of wind-blown sand blanketing the earlier deposits, while a system of shallow streams flowed off the northern slope of Anyskop, a hill on Langeberg, drawing phosphate from the Varswater Formation.

TABLE 1
Stratigraphy of the Varswater Formation and associated sediments

Age	Stratigraphic Unit		Maximum thickness	Lithology
Quaternary	Pleistocene aeolian sands		41 m	Calcareous-quartzose sands, medium- to fine-grained, moderately sorted
	River channel sediments		2 m	Greenish-white clayey sands with channels of clayey sand and phosphatic sandstone
Pliocene	Varswater Formation	Pelletal Phosphorite Member	25–28 m	Upper and lower boundaries defined as 2% P ₂ O ₅ cutoff. Moderately sorted, medium to fine phosphatic-quartzose sands. Phosphate present as sub-spherical pelletal phosphorite. Lenses and concretions of phosphatic sandstone
		Fluvial Sand Member	7 m	(i) Estuarine facies: yellowish-brown sandy silt, poorly sorted. 30–40% mud. Little phosphate. Mammal fossils abundant (ii) Fluvial facies: coarse sand intercalated with fine sand. Moderately sorted quartzose sands
		Beach Gravel Member	0,5–2 m	Consolidated quartzose sands, frequently phosphate mineralized. Well-rounded beach cobbles and gravelly-sands. Shell casts of molluscs of warm-water affinity
		Kaolinitic clay (freshwater)	6 m	Grey-black carbonaceous clay, pyrite, grass and <i>Podocarpus</i> pollens
		Quartzose sand unknown origin	?	Fine quartzose sand
UNCONFORMITY-TILTING				
Middle Miocene	Basal bed		0,5–1,5 m	Generally poorly sorted, fine-grained phosphatic-quartzose sandstone. Hoedjiespunt: massive lens of bedded apatite, less than 1% quartz
	Mottled silty-clay		?	Silty-clay, poorly sorted, iron stained. No phosphate. Extent unknown

PETROLOGY OF THE PHOSPHORITES

A detailed optical study of the phosphorite pellets and phosphatic sandstone is largely precluded because of the submicroscopic size (0,25-4 μ) of the apatite mineral and the admixture of argillaceous, carbonaceous and ferruginous impurities. The pellets may all be classified as true phosphorite, having a P_2O_5

content in excess of 18 per cent. But this does not necessarily hold true for all the phosphatic sandstone specimens, which will be described along with the true phosphorite.

PELLETAL PHOSPHORITE

The term pellet as used throughout this report is not used in a genetic sense or even restricted to particles smaller than 0,15 mm (2,740) as defined by Folk (1962). 'Pellet' is used here entirely in a descriptive sense. The mean grain-size of the pellets is coarser than that of the associated quartz grains in the sediment. The mean pellet-size on Langeberg is 2,020 (range 1,8–2,30); on Witteklip they are finer grained, 2,270 (range 1,5–2,70). North of Hondekliipbaai the pellets are typically coarser (0,5–1,50). The amount of pelletal phosphorite in silt-size grades is negligible. The pelletal particles are present in three distinct forms. Those of biogenous origin are present only in trace amounts. The inorganic pellets appear to owe their gross morphology to particle size. In the coarser fractions (2,0 to –0,50) the pellets are of platey or irregular appearance while below 2,00 ovoidal structureless pellets predominate.

The increase in degree of roundness with diminishing size displayed by the pelletal phosphorite is opposite to the trend of the quartz grains in the same sediment where roundness improves with increasing grain-size. This reversal of behaviour of the pellets is readily explained by their soft (hardness of apatite is 4,5 to 5) but brittle nature. The larger particles tend to fracture and remain subangular. Finer than 20, the phosphorite abrades more rapidly than the quartz. The spheroidal shape of the pellets results in their behaving differently from the coarser plates under turbulent conditions. The sub-spherical pellets are probably in hydraulic equilibrium with the coarser platey pellets. The high degree of rounding and sorting of the pellets is characteristic of deposition in a littoral environment.

Generally the edges of the coarser platey pellets show some signs of wear, while many of the grains have a conchoidal fracture and often a striated surface. Undoubtedly many of these grains are actually phosphatized mollusc shell fragments, but such an origin does not account for all of them as D'Anglejan (1967) suggested for his phosphorites. The pellets range in colour from pale yellow to orange to deep red. They are usually of fresh appearance and often translucent. Frequently they have white blemishes due to finely divided clay material, or are mottled black by organic carbon. Generally these grains are of lighter and more yellow coloration than the smaller ovoidal pellets. Frankel (1943) analysed the white portion of nodules from Langebaanweg as montmorillonite.

The ovoidal pellets constitute more than 90 per cent of all pellets in the 2,5–3,50 fraction. They are regular, sub-spherical in shape (Fig. 2). Rod-shaped, but nevertheless well-rounded pellets are also found. Rooney & Kerr (1967) have described similar particles with a groove running down the length of the rod, which they thought were probably minute bones, although they concede the



Fig. 2
Morphology of typical pelletal phosphorite.

possibility of coprolites in their sediments. Arakawa (1971) illustrates some faecal pellets of invertebrates which are very similar to those found in the Varswater Formation. Very rare are some well-rounded pellets composed of aggregates of smaller pellets and phosphate cemented. The ovoidal pellets are usually brown, orange or red, but black and green pellets have also been noted. Towards the base of borehole W'5 (Witteklip) the pellets are mostly black, due to large amounts of organic carbon (Fig. 6). Black mottling and white blemishes are common in most of the ovoidal pellets.

Included with the biogenous particles are translucent and opaque phosphatized echinoid spines, foraminifers, minute fish teeth, Bryozoa and coprolites. The echinoids spines generally have rounded extremities and the foraminifers (predominantly *Elphidium* sp.) also show considerable wear. The coprolites are cylindrical and usually have a groove down their length.

Because of the cryptocrystalline state of the apatite, the pellets are difficult to study in thin-section. And the poorly crystalline state results in low intensity X-ray diffractometry peaks. In thin-section the pellets are yellowish brown and isotropic to very slightly anisotropic. Some pellets have an outer rim of aniso-

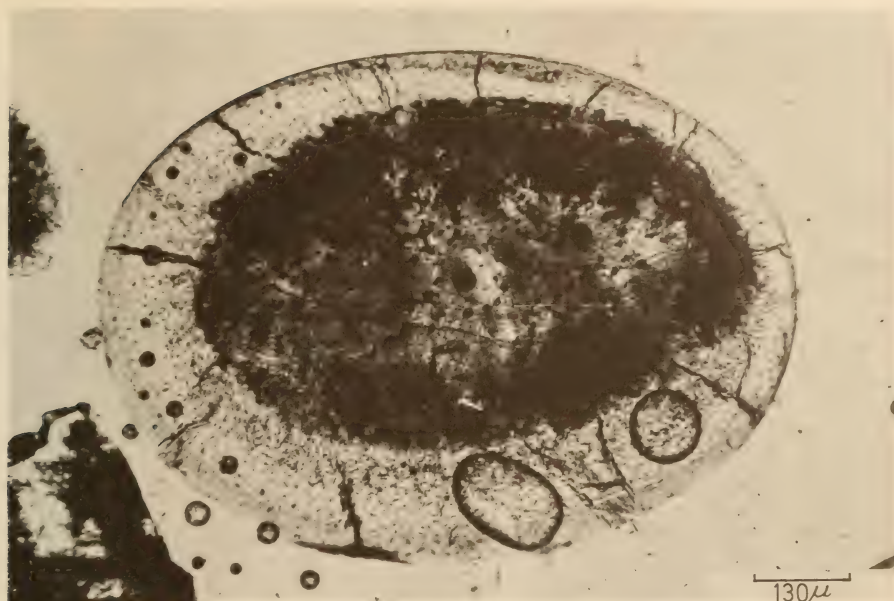


Fig. 3

Structure of pellet that has resulted from the migration of impurities away from the rim.

tropic apatite. They are usually structureless, although a structure may occur after apatite has grown about an older pellet, or the growth of the apatite crystals has pushed aside the carbon and argillaceous inclusions (Fig. 3). Frequently the pellets contain subangular silt-size quartz grains randomly scattered throughout the groundmass (Fig. 4). These frequently give the impression of a nucleus. But the presence of organic carbon and argillaceous material within pellets suggests precipitation within the pore-spaces of the sediment, the silt-size quartz being also present in these pore-spaces. (Attempts to determine the organic carbon content by direct combustion, first in an atmosphere of nitrogen, and again in an atmosphere of oxygen, produced inconclusive results. However, hydrochloric acid leaching of the apatite left behind a black fibrous organic carbon-like residue which was rapidly oxidized by peroxide.) In only one partially corroded pellet was a well-developed oolitic structure present, showing concentric shells of radiating anisotropic francolite. Figure 4 shows the occurrence of a well-rounded grain that is predominantly quartz but includes one portion of phosphorite. Although the phosphorite formed originally as an authigenic mineral within the pore-spaces of an older formation, in the latest cycle of erosion the phosphorite has become associated with the detrital components of the sediment and has been abraded to the typical pelletal form. Figure 5 demonstrates typical pellet form. It also demonstrates the ubiquitous nature of organic carbon in the pellets, and shows a pellet of biogenous origin. At the base of W'5 (Witteklip) the pellets are saturated with organic carbon (Fig. 6).

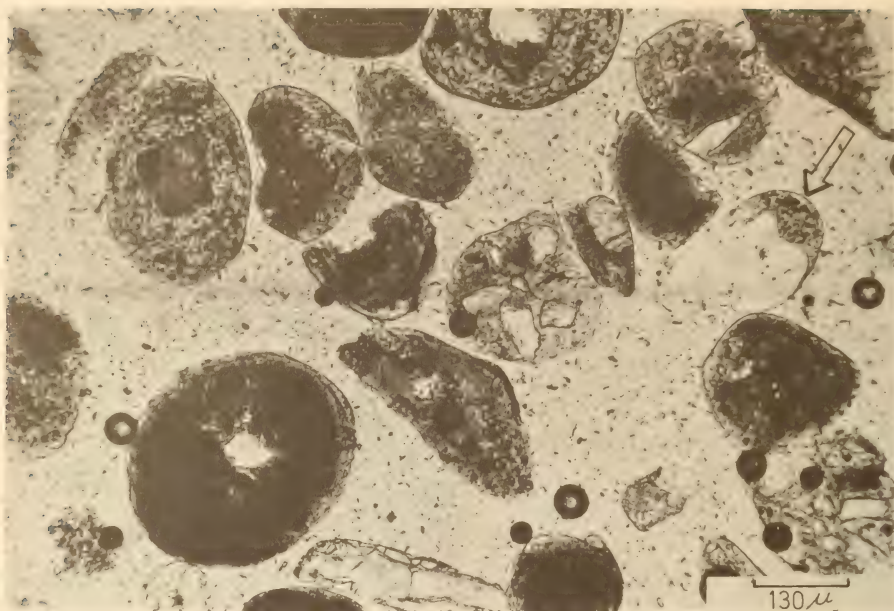


Fig. 4

Pellets with quartz grain inclusions. Arrow indicates a well-rounded grain composed of part phosphorite, part quartz.

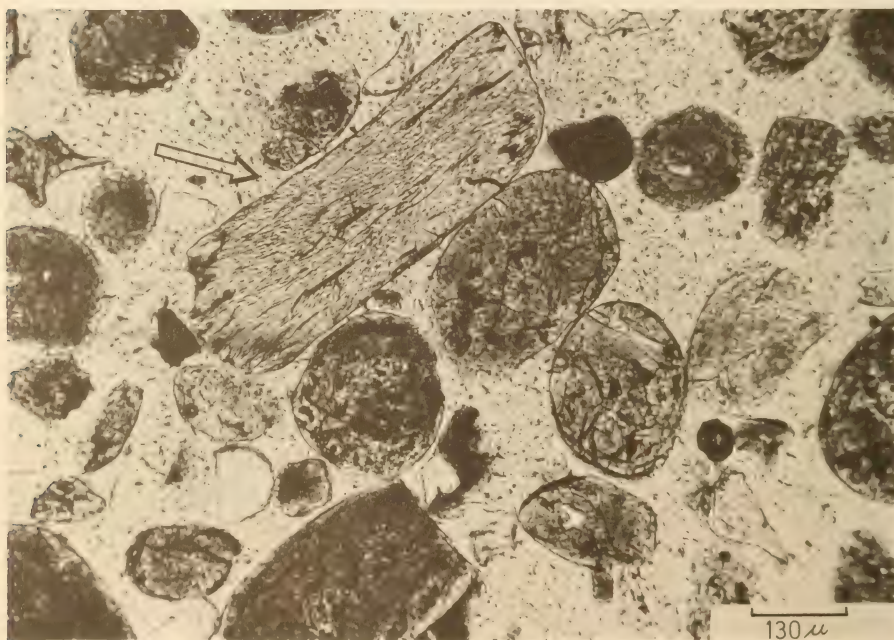


Fig. 5

Typical structure of pelletal phosphorite. Arrow indicates biogenic particle.

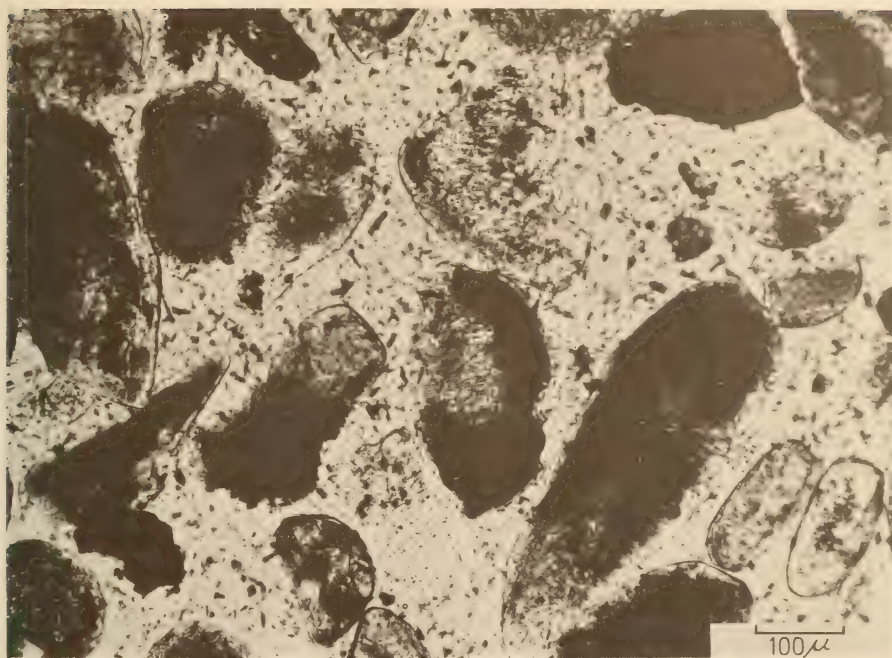


Fig. 6
Pellets coloured black due to carbonaceous material.

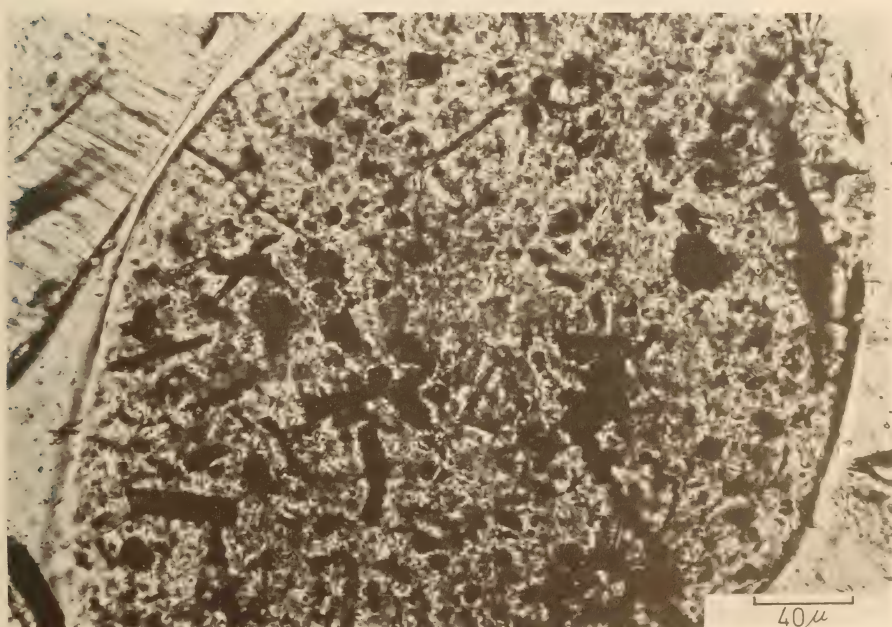


Fig. 7
Organic material present as small laths.

Many of the pellets contain small laths (Fig. 7), possibly of organic material, but it is impossible to identify them.

Phosphorite pellets with oxidized rims are common. Similar features led Rooney & Kerr (1967) to suspect extensive reworking. The ovoidal pellets have had a longer period for oxidation of the organic constituents to take place, whereas the more angular pellets have a fresher appearance due to their comparative youthfulness. The pellets owe their colour to disseminated aggregates of carbonaceous, argillaceous and ferruginous impurities. The iron oxide (Fe_2O_3) content of many pellets is as high as 3,4 per cent. Opaline silica is frequently present within the pellets, and in other cases has formed a shell about the pellet from within which the apatite has been dissolved, leaving a fragile empty shell. (D'Anglejan (1967) records a similar phenomenon.) The coarser platey pellets have in many cases a texture typical of shell debris. Some sections strongly resemble young bone or cartilage (Fig. 8) and tooth dentine (Fig. 9). It was



Fig. 8

Pellet structure resembling young bone or cartilage.

found that some of the pellets on Witteklip have a texture very similar to that of the Hoedjiespunt phosphorite. But chemical analyses show the Hoedjiespunt phosphorite to be dahllite and the Witteklip pellets predominantly francolite. The Langeberg pellets likewise have a texture very similar to that of the matrix of the local basal bed.



Fig. 9
Structure similar to tooth dentine.



Fig. 10
Scanning electron photomicrograph showing apatite crystals in phosphorite pellet.

Figure 10 shows the minute dimensions of the apatite crystallites in the phosphorite. The texture of the fracture surface of the pellets is further illustrated in Figures 11 and 12.

PHOSPHATE ROCK

Phosphatic sandstones have resulted from the precipitation of collophane (a useful term that encompasses all the cryptocrystalline carbonate apatites) within the pore-spaces of a quartzose sand. At Hoedjiespunt the phosphorite horizon, 1,5 m thick, contains less than 1 per cent quartz. Bushinsky (1966) defines phosphorite as a rock containing more than 18 per cent P_2O_5 (approximating to 50 per cent apatite). In only 38,1 per cent of the phosphatic rocks of this study did the P_2O_5 concentration exceed 18 per cent. The highest P_2O_5 value is 27,2 per cent. The average value for the basal bed is 14,9 per cent P_2O_5 . Parker & Siesser (1972) report an average of 15 per cent P_2O_5 in the continental margin phosphate rocks.

1. *Miocene basal bed*

The rock is brown with a surface that is polished and is undulating or pitted by differential erosion or burrowed by marine animals. Essentially the rock of



Fig. 11

Scanning electron photomicrograph showing structure of pellet fracture surface.

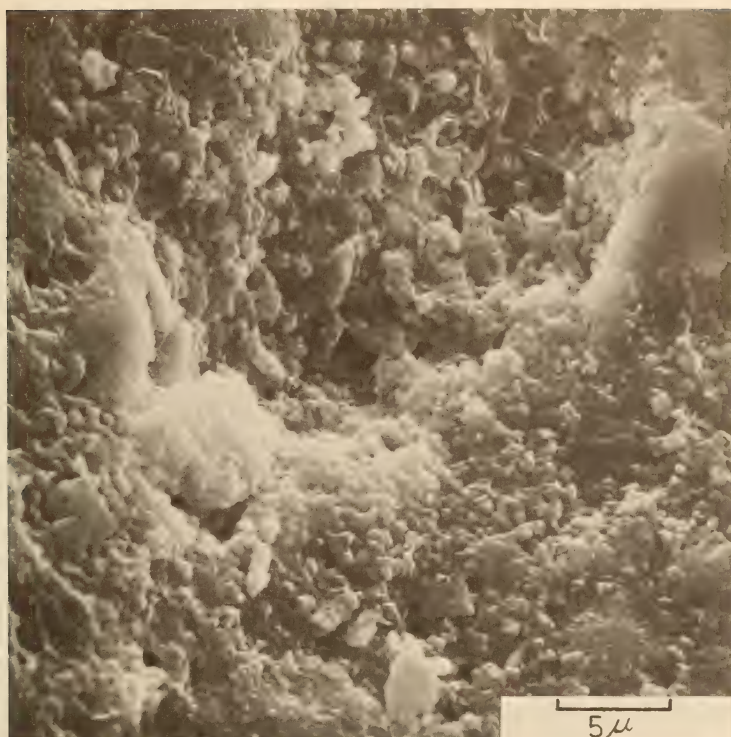


Fig. 12

Scanning electron photomicrograph showing typical structure of pellet fracture surface.

this horizon consists of fine sand-size quartz embedded in a matrix of finely divided argillaceous and organic material that is collophane cemented. Frankel (1943) has identified the argillaceous material as montmorillonite. The detrital quartz fraction constitutes from 20 to 95 per cent of the rock. It has a mixed grain population, generally poorly sorted, and frequently shows considerable iron staining. Fe_2O_3 percentage ranges from 0,3 to 6,5.

Near the south-western corner of the New Varswater Quarry the basal bed is markedly conglomeratic, and in places brecciated (Fig. 13). Fractures in the larger non-phosphatic sandstone inclusions are penetrated by collophane. These inclusions are usually rounded, while some have been almost completely phosphate mineralized. Figure 14 illustrates a rather problematical occurrence of phosphate rock. Here phosphate-rich solutions have differentially impregnated the host rock. There are no textural differences across the phosphate/phosphate-free interfaces. Most of these phosphate rocks may be described as medium- to fine-grained collophane packstones. In the majority of cases the collophane has undoubtedly originated by direct precipitation of phosphate within the pore-spaces of a quartz sand from phosphate-rich waters. But in a few cases precipita-

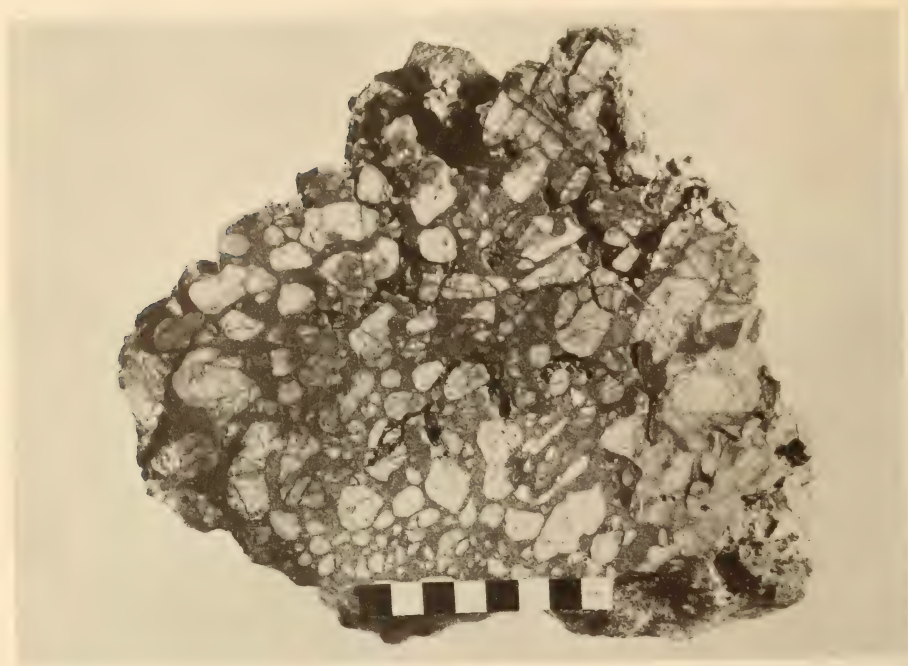


Fig. 13
Conglomeratic nature of some basal bed rock.



Fig. 14
Preferential phosphate mineralization of basal bed.

tion of the phosphate has possibly been induced by algae present in the sediment. Figure 15 shows a structure that has developed in the form of concentric shells of different mineral composition. In Figure 16, which is an enlargement of part of the previous figure, it is shown that this structure has developed independently of the basic sediment texture. The concentric shells reflect zones of enrichment by collophane and sometimes iron oxide. Iron oxide (?goethite) would appear to be ubiquitous in these phosphate rocks, but it could be younger than the phosphate component in many cases.

Heavy minerals, mainly ilmenite, are present only in trace amounts. Bone fragments, which are common, are always completely phosphatized. Shell debris is much less common.

As the amount of quartz varies considerably so does the number of inter-grain contacts. Grain contacts vary from nil to three per grain. A grain contact of one indicates an originally loosely packed sediment, while a grain contact of three per grain suggests close packing. The quartz fraction is a mixed grain



Fig. 15
Concentric structure of phosphorite.

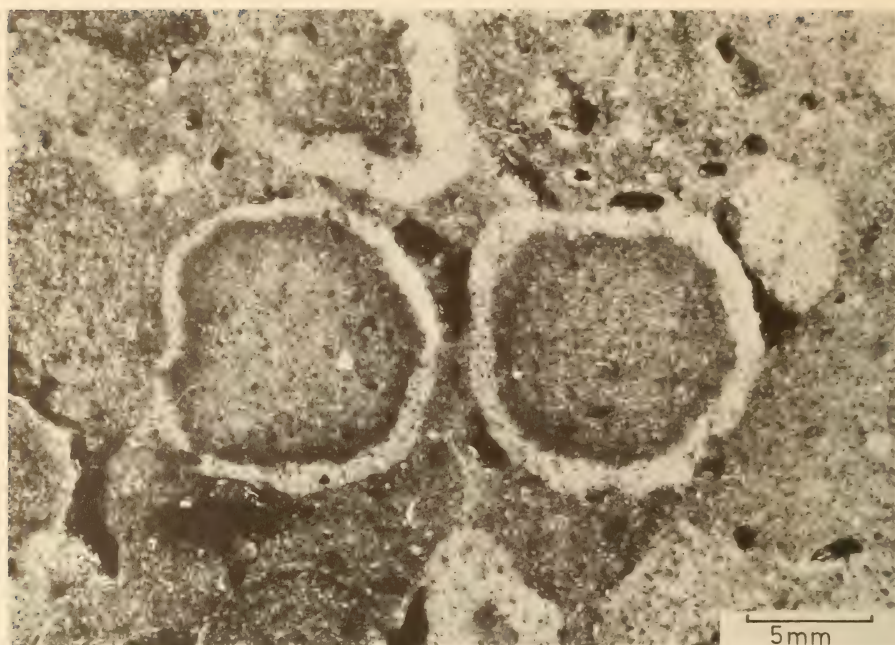


Fig. 16
Enlarged section of previous plate showing that concentric structure has developed independently of sediment texture.

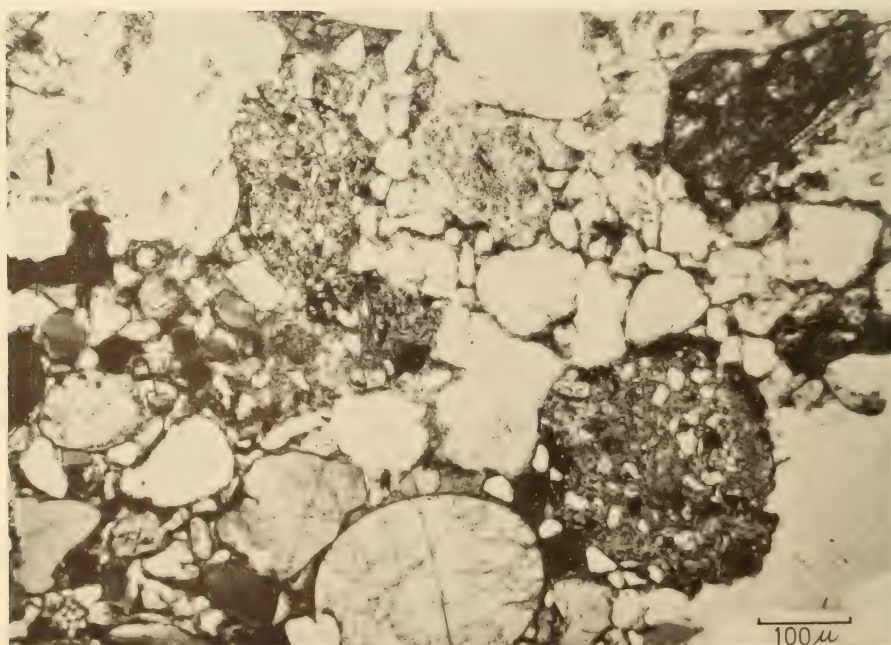


Fig. 17
Phosphorite pellets containing quartz grains in phosphatic sandstone of basal bed.

population, the largest grain-size being about 0,4 mm and well rounded. Many of these well-rounded grains have been broken in the last cycle of erosion, the rounded aspect having been inherited from a previous cycle. Corrosion of quartz grains has also occurred. An interesting feature of the phosphate rock is the frequency of pellets of phosphorite with much silt-size quartz in the matrix (Fig. 17). Some of the included phosphorite pellets are, like the quartz, corroded. Sometimes pore-spaces are lined with drusy quartz. Generally the matrix is yellow brown under plane-polarized light. It consists often of a rim of anisotropic francolite grown from the walls of the voids, the remaining space being filled with isotropic collophane. The structure suggests precipitation of the apatite in the pore-spaces of the sediment. The drusy francolite is illustrated in Figure 18. Only very seldom was any calcite found.

As the beach cobbles from the Beach Gravel Member have been derived by erosion of the basal bed, there is little that need be said about them. Thin-sections showed a composition of about 90 per cent by volume of detrital quartz, which has a close-packed structure (grain contact of 3 per grain). The matrix, as for the basal bed, is composed of isotropic or slightly anisotropic collophane.

The apatite of Hoedjiespunt has a very different aspect. The rock contains 3,6 per cent SiO_2 ; 1,8 per cent Al_2O_3 ; 0,3 per cent Fe_2O_3 and 34,0 per cent P_2O_5 . Thin-section study and X-ray diffraction data confirm that little of the SiO_2 is

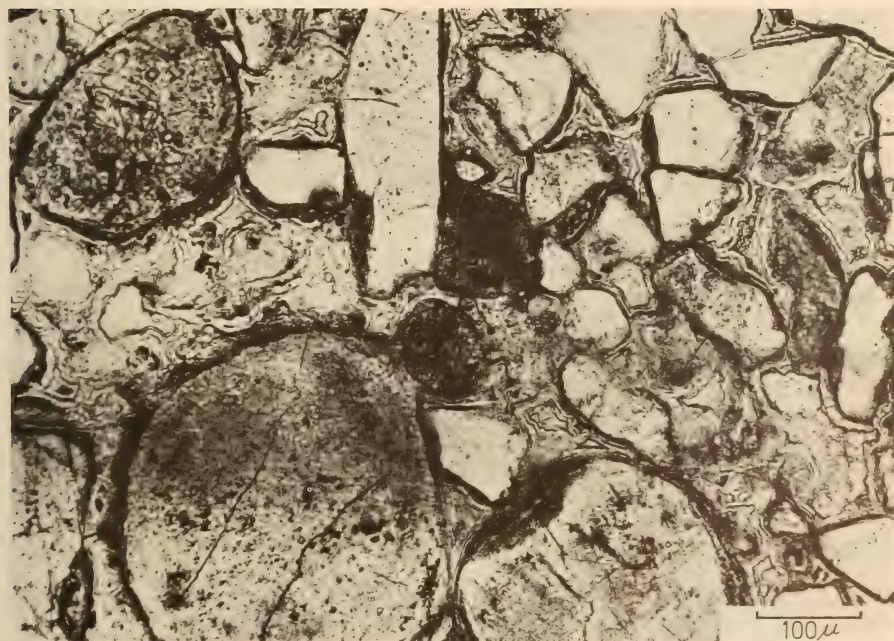


Fig. 18

Drusy francolite grown from walls of the voids in the phosphatic sandstone.

present as free quartz. Even the clay mineral that accounts for the balance of the SiO_2 and Al_2O_3 is present in very small amounts. The low fluorine content defines the mineral as dahllite. Like the francolite of Langeberg it is isotropic to very slightly anisotropic under crossed nicols. Shell debris, bryozoan remains and foraminifers are set in a collophane (dahllite)/micrite groundmass (Fig. 19). The concentration of iron oxide is considerably lower than that of the Langeberg basal bed. Planktonic foraminifers are present. The Hoedjiespunt phosphorite is partly phosphatized micrite and partly phosphatized microcoquina. Figure 20 shows small cleavage flakes of phosphorite set in a collophane matrix, while there has also been collophane precipitation along fractures within the initial collophane matrix. An oolitic structure is shown in Figure 21. This type of structure is common in the Hoedjiespunt phosphatized wackestone.

2. Phosphate rock of the Varswater Formation

Precipitation of isotropic collophane within the pore-spaces of the quartz sands has been influenced by local concentrations of organic matter. This has resulted in the development of thin lenses and concretions of phosphatic sandstone. Figure 22 shows a tortoise bone that has acted as a nucleus for phosphate deposition which has followed the contours of the bone. Although the bone is completely phosphatized, the maximum phosphate deposition outside the bone



Fig. 19
Hoedjiespunt phosphorite showing foraminifers and shell debris.

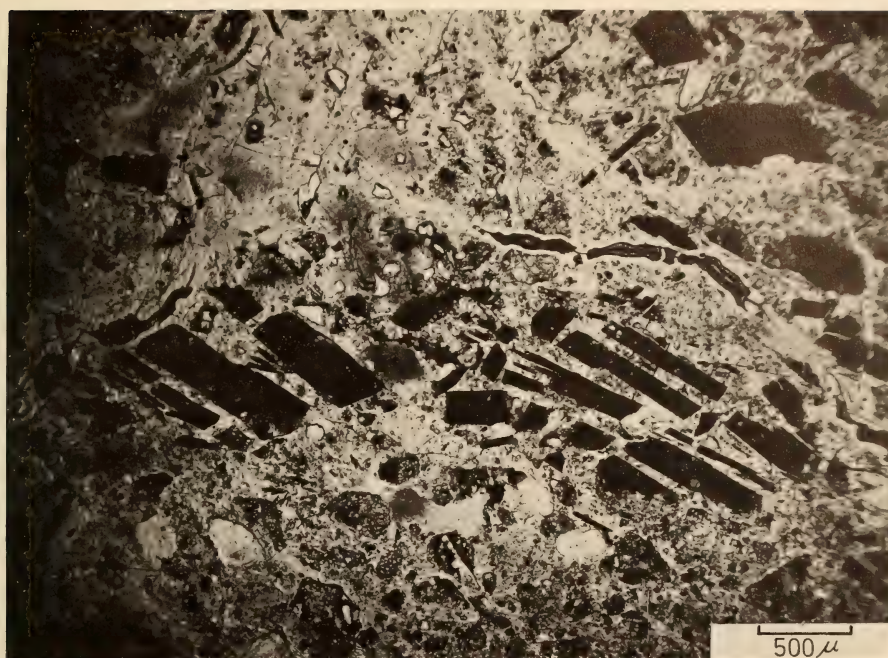


Fig. 20
Older flakes of phosphorite in phosphorite groundmass, Hoedjiespunt.

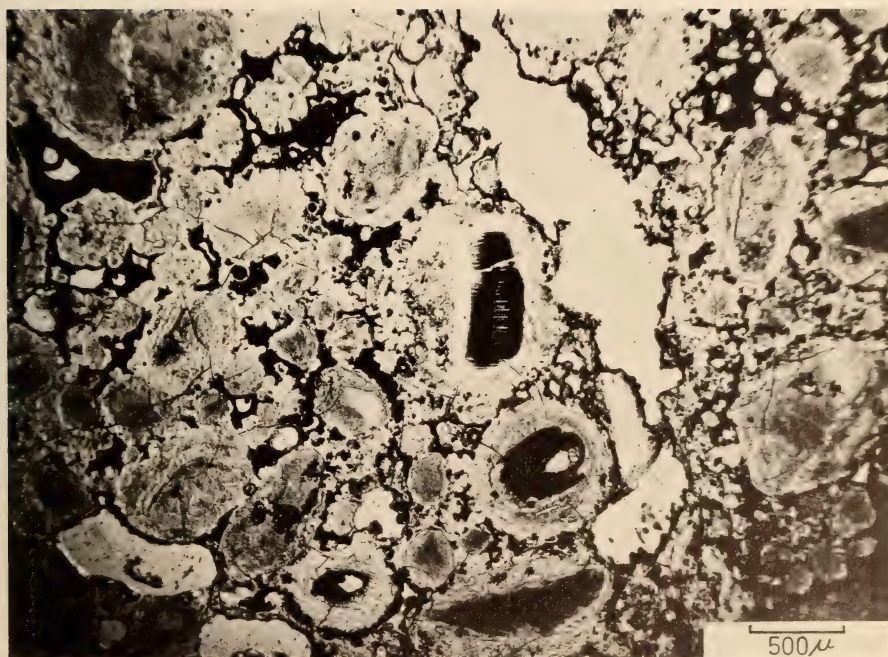


Fig. 21
Oolitic structure, Hoedjiespunt.

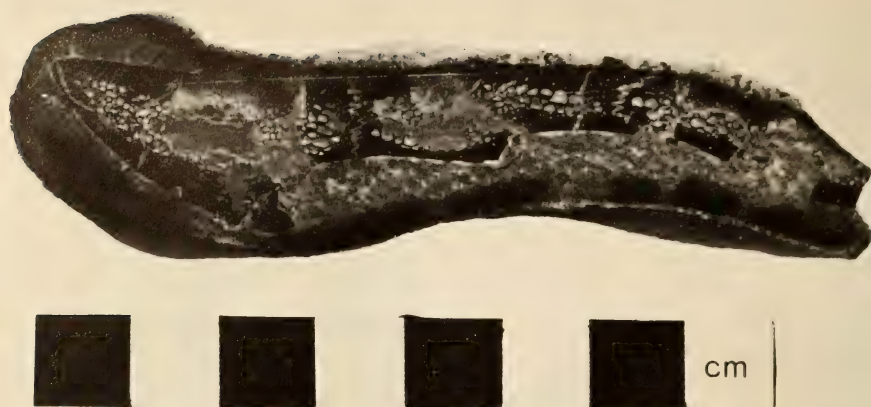


Fig. 22
Tortoise bone that has acted as a nucleating centre for phosphate precipitation.



Fig. 23
Typical phosphatic sandstone lens structure from Varswater Formation.

is slightly separated from the bone itself. Figure 23 shows the type of local concentration of phosphate frequently encountered. The detrital components of the phosphatic packstones are always similar to that of the surrounding sediment, and they include also phosphorite pellets. Cementation has taken place by precipitation of francolite about the grains to give a radially disposed cryptocrystalline francolite with the pore-spaces filled with clear collophane or mud. Only occasionally is drusy quartz found. In some of the packstones a crudely graded bedding has been observed. The colour of these phosphatic packstones ranges from pale brown to black. Samples from borehole S12 (42,8 m) were analysed. The brown variety contained 11,6 per cent P_2O_5 and the black variety 19,6 per cent P_2O_5 . Towards the base of the Varswater Formation a collophane mudstone is frequently encountered (Fig. 24). It contains 5 to 10 per cent detrital quartz set in a fine phosphatized argillaceous matrix.

MINERALIZATION

Petrographic evidence suggests that at least three distinct periods of post-depositional phosphatization have occurred. The conglomeratic phosphate rock



Fig. 24
Collophane mudstone.

or packstone of the Langeberg basal bed shows two periods of mineralization. The first phase is represented by fragments of an older phosphate rock as well as phosphorite pellets. These older components were reworked and deposited to form a new rock mass which has subsequently become phosphatized. In the basal bed phosphate precipitation has resulted in a phosphate packstone only one metre thick. Phosphate mineralization must have taken place fairly rapidly after deposition. The presence of phosphatized cartilage or young bone material would also suggest that very rapid phosphatization has occurred. Phosphatization of the basal bed must have been nearly contemporaneous with sedimentation and must have depended upon the close proximity of upwelling of phosphate-rich water (to be discussed later). Phosphatization appears to be nearly uniform through much of the rock of the basal bed, although contact with phosphate-rich water has increased the degree of phosphatization in a thin layer at the surface. The overlying phosphatic packstone cobbles are identical with the basal bed and have been formed from material from that bed, which suggests that the phosphatization must have preceded the last phase of erosion. On Langeberg phosphate mineralization has taken place within the pore-spaces of a quartz sediment, mineralizing the argillaceous material already there. Organic matter within the argillaceous material has probably behaved as a catalyst. On Langeberg there is little evidence that this mineralization has proceeded via a lime replacement mechanism. I have suggested that locally the phosphate precipitation has possibly been induced by algae. The algae would have behaved in a similar way to the other organic matter. On Langeberg the phosphorite pellets of the Varswater Formation have a very similar aspect to that of the matrix of the basal bed, although some do show concentric layering. In these rare cases the concentric structure is probably the result of apatite growth about an initial pellet. There is no evidence to suggest growth of the pellets about nuclei, although silt-size quartz inclusions give the impression of nucleation. Thin-section analyses show that the quartz was present in the matrix of the original phosphorite, as was the organic material. Summerhayes (1970) argues that if the francolite in the original phosphatic rock has grown from the walls of the voids, these layers may act as lines of structural weakness. Disintegration along such lines leads to the formation of pellets of collophane that contain impurities but have a clear collophane margin.

On Langeberg the third phase of phosphate mineralization is marked by the appearance of phosphatic sandstone lenses and concretions in the Varswater Formation. The estuarine sediments are capped by a thin phosphatic sandstone horizon. In the Pelletal Phosphorite Member the phosphatic sandstone lenses and concretions include pelletal phosphorite in the same abundance as the adjoining sediments. In this same member there are phosphatized foraminiferal tests, indicating a lime replacement mechanism. Shell material, shark teeth, bone fragments, echinoid spines and foraminiferal tests are all well phosphatized.

On Hoedjiespunt the bedded apatite also demonstrates three phases of

phosphate mineralization. An original flaky phosphorite has been incorporated into a later wackestone which has been phosphatized, and in a third phase of mineralization fractures within this phosphatized wackestone have been the sites of phosphate deposition. At Hoedjiespunt it would appear that the phosphorite has resulted from colophane replacement of a micrite containing shell debris and foraminiferal tests.

Within the Varswater Formation sedimentation appears to be confined to deposition of fine material. Frequent erosional episodes have resulted in concentration of shark teeth and mollusc shells into definite horizons. Widespread reworking is attested by the broken detrital grains and shell debris and worn foraminiferal tests. All evidence suggests low rates of sedimentation.

CHEMICAL COMPOSITION OF THE PHOSPHORITE

The apatite mineral of all the pelletal phosphorites and the Langeberg basal bed is francolite, while the apatite of the Hoedjiespunt phosphorite is dahllite (Tankard 1974). *Francolite* is the name applied to an apatite containing appreciable CO_2 and more than 1 per cent fluorine, whereas the name *dahllite* has been applied to apatite containing abundant CO_2 but less than 1 per cent fluorine (McConnell 1938).

Table 2 shows the chemical composition of pelletal phosphorite and Hoedjiespunt phosphorite. The high SiO_2 content of the pelletal phosphorite sample is deceptive in that it is a measure of the efficiency of the heavy liquid separation. However, the results do give an idea of the chemical constitution of the phosphorite. But much of the SiO_2 is bound up as a clay mineral where it would be combined with the Al_2O_3 and K_2O . The Fe_2O_3 content is high. Thin-section examination shows that less than 1 per cent of the SiO_2 in the Hoedjiespunt phosphorite is present as free quartz.

TABLE 2
Chemical composition of the phosphorite

	Pelletal phosphorite	Hoedjiespunt phosphorite
	%	%
SiO_2	4,13	3,60
Al_2O_3	1,73	1,83
Fe_2O_3	1,77	0,27
CaO	46,97	46,04
MgO	0,28	2,32
Na_2O	0,68	1,27
K_2O	0,26	0,06
H_2O^+	2,43	—
H_2O^-	0,44	2,55
P_2O_5	33,16	33,97
CO_2	3,81	3,28
F	3,44	0,57
SO_3	0,17	0,44
Total	99,27	96,20

Analysts: Pelletal phosphorite—General Superintendence Co.

Hoedjiespunt phosphorite—Anglo American Research Laboratories.

ALUMINIUM PHOSPHATES

The aluminium phosphates will be discussed only briefly as they are not directly related to the marine phosphorites, although both were related to the upwelling of phosphorus-rich waters. These aluminium phosphates have been described in some detail by Du Toit (1917) and Hutchinson (1950).

The aluminium phosphate distribution map (Fig. 25) shows how outcrops of the phosphate rock occur sporadically about granite hills north and south of Saldanha Bay. They are not confined to any particular altitude. The degree of phosphatization is very variable over the area and even varies within any particular hand specimen. On Konstabelkop the phosphate rock is hard and of

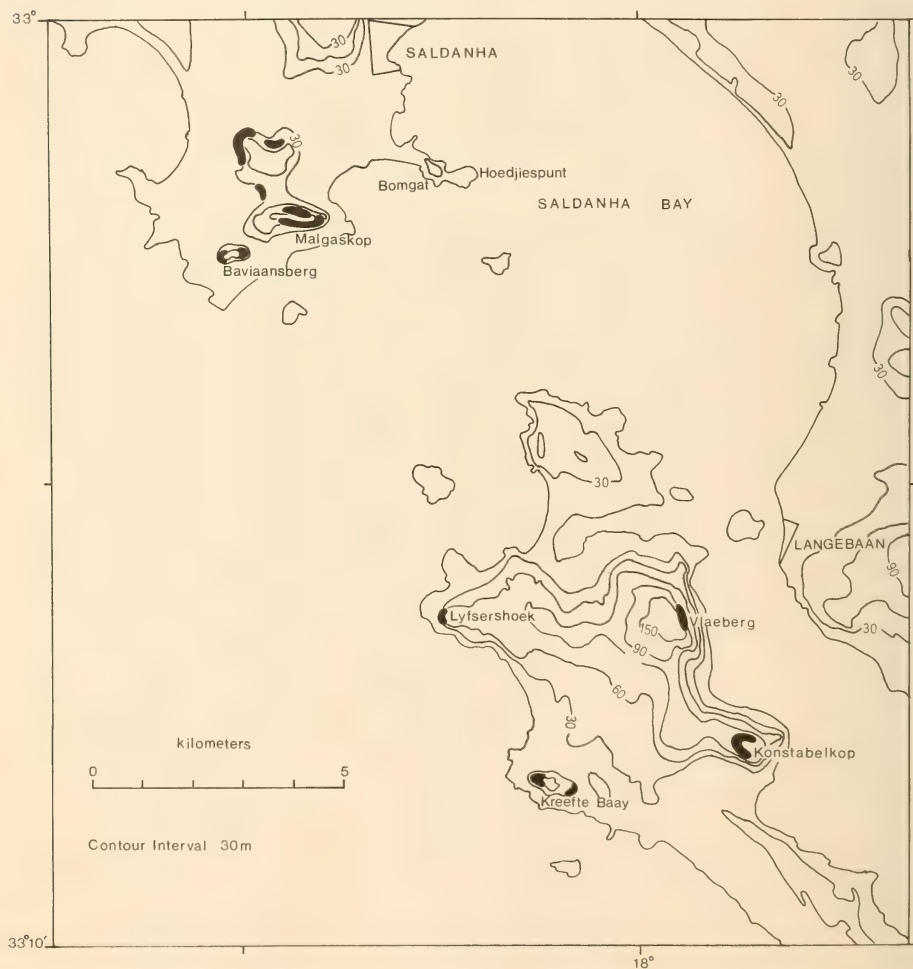


Fig. 25
Distribution map for aluminium phosphate.

moderate yellowish brown (10YR 5/4) coloration, while the phosphatized clay of slickensides is greyish brown (5YR 3/2). North of Saldanha Bay the phosphate rock has a green hue. On Konstabelkop an exploration pit in a marine terrace at 152 m a.s.l. shows rounded boulders lying on weathered porphyry. Both the underlying porphyry and the rounded boulders have been phosphatized, but in the case of the boulders the degree of phosphatization is greatest near the surface, suggesting post-depositional phosphatization.

In the main quarry on Konstabelkop the highest concentration of P_2O_5 is close to the surface, the concentration decreasing irregularly with depth. The maximum depth ranges from 1,5 m to 12 m, the base being highly irregular. At the surface weathering has produced a laterite-like layer.

The numerous slickensides, along which phosphatization is extensive, are a feature of the Konstabelkop phosphate rock. In thin-section it is seen that the groundmass is a fine clay material which has been phosphatized. The phosphatized parts of the clay are isotropic while slight anisotropism is evident at the contact of the phosphatized and unphosphatized clay. Larger quartz grains are generally fractured and have fissures filled with the same isotropic phosphate mineral. The faulting appears to have followed the phosphate mineralization since the texture of the rock shows the drag effect of movement along the fault plane. The clay minerals must originally have developed along joint planes in the granite. A detailed thin-section study was carried out and reported by Du Toit (1917).

The altitude of the phosphate deposits is very variable (as shown in Fig. 25) and cannot be related to any particular sea level as Visser & Schoch (1973) maintain. On Baviaansberg within the grounds of the Naval Academy (SAS SALDANHA) the phosphates occur at 45 m a.s.l. and have imparted a green coloration to the granite. On Malgaskop the phosphates range from 40 to 100 m a.s.l. The lower limits of these phosphate deposits are not significant as they have originated by percolating solutions.

TABLE 3
Partial chemical analyses of the aluminium phosphate rock.

	Phosphatized porphyry	Phosphatized porphyry	Yellow sandy regolith	Phosphatized limestone
	%	%	%	%
SiO ₂	59,20	65,40	10,72	10,70
Al ₂ O ₃	8,32	6,78	31,11	5,66
Fe ₂ O ₃	4,02	5,29	7,14	0,43
CaO	0,10	—	0,42	40,90
K ₂ O	0,60	0,48	2,41	0,60
P ₂ O ₅	12,14	11,68	18,31	0,92
CO ₂	—	—	—	31,40
F	Trace	Trace	Trace	Trace

Analyst: A.E. & C.I. Ltd. Results supplied by Mr Botha of the Konstabelkop Mine.

Partial chemical analyses of the phosphate rock are listed in Table 3. Several significant features are apparent:

- (1) The Fe_2O_3 content is high on the granite areas but insignificant on the phosphatized limestone.
- (2) Al_2O_3 is highest in the yellow sandy regolith (31,11 per cent). Also in this horizon the Fe_2O_3 value is highest (7,14 per cent).
- (3) Fluorine is always present in only trace quantities.

The yellow sandy regolith has resulted from lateritic alteration of the underlying phosphatized granite. Under normal soil-forming processes weak solutions from the leaching of the rock evaporate and the least soluble components precipitate first. These include hydroxides of iron and aluminium, silica and carbonates. Further solution leaves behind the aluminium and iron hydroxides in an insoluble state.

GENESIS OF THE PHOSPHATE DEPOSITS

PHOSPHORITE

Authigenic phosphorites are the subject of a voluminous literature and many authors have remarked on the close relationship between phosphorite deposits and areas of active upwelling of nutrient-rich water (McKelvey *et al.* 1953; McKelvey 1959, 1963; Sheldon 1964; Tooms *et al.* 1969). Since very few phosphorites are known to be forming at present, the origin of the phosphorite can only be inferred from the geologically young deposits. Geologically young phosphorite is commonly found in sediments adjacent to areas of modern oceanic upwelling (McKelvey 1963). These are mainly on the west coasts of continents but also to a limited degree on other coasts. Such areas of active upwelling and phosphorite occurrence lie between the 40th parallels (Sheldon 1964), e.g. south-western Cape Province, Morocco, South America, California. Ancient phosphorites on the other hand are found at higher latitudes, their present distribution being the result of continental drift. Pevear (1966) has shown that upwelling is certainly not a prerequisite for phosphate enrichment. He has suggested an estuarine origin for the phosphate of the Phosphoria Formation of the U.S.A. Such an estuarine environment would be an area of high biologic productivity.

Brongersma-Sanders (1957) has related marine mass mortalities, and phosphorite deposition, to regions of upwelling. Accumulation and decay of organic matter in the oceans at depths below 500 m concentrate phosphorus, and with upwelling caused by trade-winds blowing the surface water offshore, the phosphorus-rich water is brought to the surface, where deposition of phosphorite occurs. Precipitation of the phosphate occurs when the amount of phosphate supplied exceeds the saturation value of the sea water (Bushinsky 1966). Precipitation of the phosphorite from such saturated water is accelerated by increased temperature and pH (Sheldon 1964). A rise in temperature drives off CO_2 , which

results in a rise in pH. A low rate of supply of terrigenous detritus is very important (Pevear 1966). Tooms *et al.* (1969) have found a close association between ancient phosphorites and arid areas. Such areas would also be expected to have low or negligible rates of sedimentation and are usually associated with coasts with active upwelling. Bushinsky (1966) and D'Anglejan (1967) suggest that phosphorites have formed in water shallower than 100 m, while Parker & Simpson (1972) have found the greatest concentration of phosphate nodules on the Agulhas Bank between 100 and 140 m.

The phosphorites of the Langebaanweg-Saldanha area have much in common with other phosphorite deposits. The phosphorite occurs authigenically in the Miocene basal bed. Although this horizon has been truncated at 30 m above sea-level it has been inferred that marine limestone at 56 m above sea-level north of Saldanha represents the farthest inland extent of that sea (Tankard *in press*). At Hoedjiespunt the phosphorite occurs at 5 m above sea-level, suggesting that the depth of water at time of formation was about 50 m.

A common characteristic of phosphorite accumulations is their location on one side of a basin where deep phosphate-rich waters are upwelling adjacent to a shallow shelf (Blatt *et al.* 1972). Although uneconomic concentrations of phosphorite do occur on the open Atlantic coast between Saldanha Bay and St. Helena Bay, the highest concentrations are found in the erosional basin between Langebaanweg and Saldanha. The nearly ubiquitous presence of organic matter within the pellets suggests high productivity and a common origin for the organic matter and the phosphorite. At the base of the Varswater Formation on Witteklip the pelletal phosphorite is black due to excessive quantities of carbonaceous matter (Fig. 6). The quantity of organic matter in the phosphorite decreases upwards in the sedimentary sequence, and there is also a decrease in organic matter in the phosphorite in the Langeberg direction, resulting in lighter-coloured phosphorite. The trend is for a decrease in carbonaceous phosphorites shoreward. Commenting on an identical situation in the Phosphoria Formation (U.S.A.) Gulbrandsen (1969) notes: 'Although the locus of major apatite production is coincident with the locus of organic-matter accumulation, as exemplified by the black carbonaceous phosphorites of the Phosphoria Formation significant production can occur shoreward, where the organic matter is largely destroyed, and form light-colored, low-organic-content phosphorites such as indicated by the facies of the Phosphoria Formation. . . .' Summerhayes (1973) notes that the only significant local concentration of phosphate on the Agulhas Bank, other than that provided by the erosion of Tertiary phosphorite, is in sediments enriched in non-skeletal organic matter.

If the phosphorite can be attributed to upwelling of cold, nutrient-rich water, then it is also likely that the coastlands were as arid as at present. The average annual rainfall for this area is about 260 mm, which occurs fairly steadily in the winter months, and continental run-off is low. The relatively low winter rainfall, low run-off, and the low-lying nature of the Sandveld would promote low sedimentation rates. The intermittent reworking of the basal bed

deposits and the high grades of phosphate suggest an environment of negligible sedimentation.

In the Miocene basal bed on Langeberg the phosphorite occurs as an interstitial component of a quartzose sandstone (packstone). Frequently the phosphorite occurs as drusy-encrustations about the quartz grains, indicating crystal growth from the grain surfaces, the remaining voids are filled with clear collophane and argillaceous and organic material. The structureless aspect of the phosphorite pellets, the rare occurrence of nuclei and the mixing of collophane with organic, argillaceous and ferruginous material suggest precipitation within the interstices of the sediment. Ames (1959) found that the replacement of calcium carbonate was possibly the only way in which the carbonate fluorapatites could form. Rooney & Kerr (1967) have suggested that the North Carolina phosphorite probably originated by replacement of calcareous matter and by chemical precipitation under reducing conditions in a large, shallow lagoon or estuary with a restricted circulation. Pevear (1966) suggests that the reason why phosphorite is not forming today in Georgian estuaries is because virtually no calcium carbonate is forming at present. Thin-section study of the Langeberg basal bed rock has shown no evidence of a replacement mechanism, although phosphatization of the calcite foraminiferal tests and mollusc shell fragments demonstrate that such replacements have taken place in the overlying strata. At Hoedjiespunt the apatite has only 3,60 per cent SiO_2 , 3,20 per cent of this probably being bound up with Al_2O_3 as a clay material. Thin-section study confirms that there is less than 1 per cent quartz. It is quite conceivable that the carbonate apatite, in this case dahllite, originated by replacement of micrite and micro-coquina. The negligible amount of quartz suggests extremely low sedimentation rates in a sheltered environment. Tooms *et al.* (1969) have shown that the synthesis of carbonate apatite from solution means that the prior existence of calcium carbonate is not a prerequisite to formation of this mineral. At Hoedjiespunt the phosphorite has an oolitic structure in places while some structures in the basal bed at Langeberg suggest that precipitation by algae has played a small part. Charles (1953) has attributed much phosphorite formation to precipitation by algae.

Summerhayes (1970) has noted the limited evidence for contemporaneous formation of carbonate apatite, there being very few submarine phosphorites of recent age. McKelvey *et al.* (1953) found no bedded phosphorites younger than late Tertiary. The environmental conditions most favourable to phosphorite formation occurred in the warmer mid Tertiary seas (Tooms *et al.* 1969). Baturin (1971) has shown some evidence of phosphorite forming at present along the South West African coast, these sediments being further discussed by Summerhayes *et al.* (1973).

Haughton (1932) attributed the phosphorites of Langebaanweg to alteration of a calcareous deposit by phosphatic solutions. He thought the aluminium phosphate and the phosphorite had a similar phosphate source, in that both were derived from organic masses such as guano. Haughton saw three possible

ways in which the phosphate could have arrived in the sediments at Langebaanweg;

- (1) the phosphate was derived from the guano deposits about Vredenburg by percolating waters
- (2) the area in question could be covered by continuously replenished guano-dust blown in by west winds
- (3) the guano was deposited on islands at Langebaanweg, but he notes that no evidence of the guano can be found in the area.

If the phosphate was transported by groundwater from Vredenburg it must be remembered that the Langeberg deposits are 13 km from that area. It has already been shown that the phosphorite is essentially a basin deposit in the study area, and that maximum concentration of phosphorite is about the perimeter of the basin. Groundwater from Vredenburg would have had to phosphatize selectively the periphery of the basin. Phosphorite deposits are also found along the Namaqualand coast where topography is not conducive to guano accumulation.

The phosphate is unlikely to have been transported as a fine guano-dust since westerly winds blow only in the wet winter months in the south-western Cape, and are rain-bearing. Dust is unlikely to be transported in large quantities during this season. Furthermore, guano deposits do not lend themselves easily to dust formation on the scale envisaged.

Certainly on the granite hills north and south of Saldanha Bay percolating phosphate solutions have produced aluminium phosphates. The mineral produced has depended entirely upon the rock being phosphatized, e.g. on Konstabelkop the phosphatization of the granite and limestone. On Witteklip-Sandheuwel the phosphorites are banked against the same granite masses but now the phosphate is a carbonate fluorapatite just as at Langeberg. Similarly the phosphorite at Hoedjiespunt is a carbonate apatite, although it rests on a granite shelf which it has phosphatized. It has been shown that the basal bed at Langeberg contains the phosphorite as an interstitial material and that there is no evidence of calcium carbonate replacement. Chemically the pelletal phosphorite of the Varswater Formation and the aluminium phosphates of the granite terrain are totally different. The phosphorite characteristically has a higher F content, while the aluminium phosphates contain higher concentrations of Al_2O_3 and Fe_2O_3 . If these deposits had a similar origin then the pelletal phosphorites should include an aluminium-rich component. Frankel (1943) has noted the small percentage of iron and aluminium phosphates. Frankel suggests that the sources for the fluorine must be found in either the sea or the granitic areas. The latter option must be discarded since the aluminium phosphates on the granitic rocks are notably poor in fluorine. Frankel concludes that phosphatic solutions in percolating through these deposits 'converted the limestones and calcareous nodules into (probably) hydroxy-apatite and the argillaceous rock types into aluminium and iron phosphates.

ALUMINIUM PHOSPHATE

The aluminium phosphate on the granite hills north and south of Saldanha Bay is very different from the marine phosphorites of the Varswater Formation, although it, too, can be related indirectly to upwelling phenomena. The upwelling of nutrient-rich waters forms a food chain upon which great colonies of sea-birds thrive. The largest guano deposits are found associated with such areas (Hutchinson 1950). On the Cape west coast the most important guano birds are *Morus capensis* (Cape gannet), *Spheniscus demersus* (jackass penguin) and *Phalacrocorax capensis* (Cape comorant). Seabird guano is a richly nitrogenous phosphorus material, the phosphate concentration increasing as the more soluble nitrates are leached out. Flack (1916) reports the total nitrogen and P_2O_5 contents of mixed guano from Malagas, Marcus and Jutten Islands (Fig. 1) as 10,94 per cent and 13,80 per cent respectively. CaO for this sample was 12,49 per cent. 4,11 per cent of the P_2O_5 was water soluble, the rest being acid soluble. Fresh guano is characteristically rich in nitrogenous phosphorus, but with leaching of soluble nitrates the P_2O_5 concentration increases. Low-pH waters transport the phosphate from the guano to the bedrock where it reacts to form new minerals. Thus reaction with limestone has produced calcium phosphate and reaction with clay minerals formed along joint planes in the granite on Konstabelkop has produced the aluminium phosphates. Whereas the phosphorites have high carbonate and fluorine contents, these are dependent entirely upon the type of rock that is being phosphatized in the case of the aluminium phosphates. Although the original source of the phosphate can be attributed to guano accumulations, direct evidence of a guano deposit has been destroyed by weathering. The formation of phosphorite, on the other hand, appears to be largely due to precipitation from phosphate-rich sea water. At Hoedjiespunt the phosphorite has resulted from post-depositional phosphate mineralization of a micrite and microcoquina. While the precipitation of the phosphorite is temperature and pH dependent, the aluminium phosphates appear to be dependent upon large seabird colonies. Upwelling of nutrient-rich waters could at present sustain vast seabird colonies but so far there is no evidence of phosphorite deposition. Thus, although the two phosphate deposits are dependent upon the upwelling, there is no reason why the phosphorites and aluminium phosphates should be related in time. It is more likely that the aluminium phosphates are derived from leaching of guano deposits which have accumulated over a considerable length of time. Visser & Schoch (1973) believe that these phosphates can be correlated with particular sea-levels, but if they owe their origin to seabird colonies no such relationship seems likely.

According to Harrington *et al.* (1966) aluminium phosphates result from the solution and transportation of phosphate minerals from phosphatic limestone or guano by low-pH waters in hot humid regions. Hutchinson (1950) and Harrington *et al.* (1966) have shown that the largest guano deposits are found in the vicinity of the same regions of upwelling of cold phosphorus-rich water as the marine phosphorites. Harrington *et al.* infer that where the bedrock consists

of silicates the phosphate will form a variety of aluminium silicate minerals, such as variscite or metavariscite and crandallite. Du Toit (1917) found that the average composition of the Konstabelkop phosphate is close to that of barrandite while minute yellowish crystals may be referred to wavellite or variscite. Altschuler *et al.* (1956) have found that the upper part of the Pliocene Bone Valley Formation, Florida, has been altered to aluminium phosphate in a zone averaging about 2 m in thickness. This alteration has taken place by weathering and groundwater which has produced a progressive change in mineralogy with depth. They found that the top of the zone is characterized by the aluminium phosphate wavellite while the middle zone is characterized by the calcium aluminium phosphates crandallite and millisite. Both crandallite and millisite are virtually isotropic. The Bone Valley phosphates are characterized by higher CaO and F than the Konstabelkop phosphates.

SUMMARY

Bedded marine phosphorites of late Tertiary age are found today in warm climates between the 40th parallels in areas adjacent to divergent upwelling of nutrient-rich waters. Precipitation of the phosphate is dependent upon an increase in temperature as the upwelling water reaches the surface, and low rates of supply of terrigenous detritus. At Langeberg a consolidated phosphatic sandstone of Miocene age has formed by precipitation of the phosphate (francolite) in the voids of a marine sand. The francolite is associated with finely divided argillaceous, ferruginous, and carbonaceous material. On Hoedjiespunt, on the other hand, the bedded apatite contains a total of only 3.6 per cent SiO_2 , most of this being present in a clay mineral. The Hoedjiespunt apatite is defined by the concentration of fluorine and carbonate as dahllite. At both Hoedjiespunt and Langeberg sedimentation rates were very low in a sheltered environment. In the phosphatic sandstone at Langeberg the francolite has grown from the quartz grain surfaces, the voids being finally filled with isotropic collophane. The basal bed also shows reworking of the sediment, and possibly precipitation by algae.

Deposition of the Miocene basal bed was followed by a period of emergence. Then in the Pliocene the basal bed was partially reworked by a further transgression, and the Varswater Formation deposited. Erosion of the basal bed liberated the matrix material, which then became associated with the detrital component of the Varswater Formation as pelletal phosphorite. The pelletal phosphorite is very similar to the authigenic phosphorite of the basal bed in texture. It contains much argillaceous, ferruginous and carbonaceous material as well as silt-size quartz particles. Also included with the pellets are biogenic remains, foraminiferal tests, minute fish teeth, etc. It was shown that the highest organic carbon content is found at the base of the Pelletal Phosphorite Member on the seaward side of the basin, and that organic carbon content decreases shoreward.

The phosphorite deposits are briefly compared with the aluminium phosphates which occur on the granite hills north and south of Saldanha Bay. Whereas the phosphorite has formed as a marine precipitate, the aluminium phosphates probably originated by leaching of guano deposits and subsequent reaction of these solutions with the bedrock.

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Anthony J. Tankard

PETROLOGY AND ORIGIN OF THE PHOSPHORITE
AND ALUMINIUM PHOSPHATE ROCK OF THE
LANGEBAANWEG—SALDANHA AREA,
SOUTH-WESTERN CAPE PROVINCE

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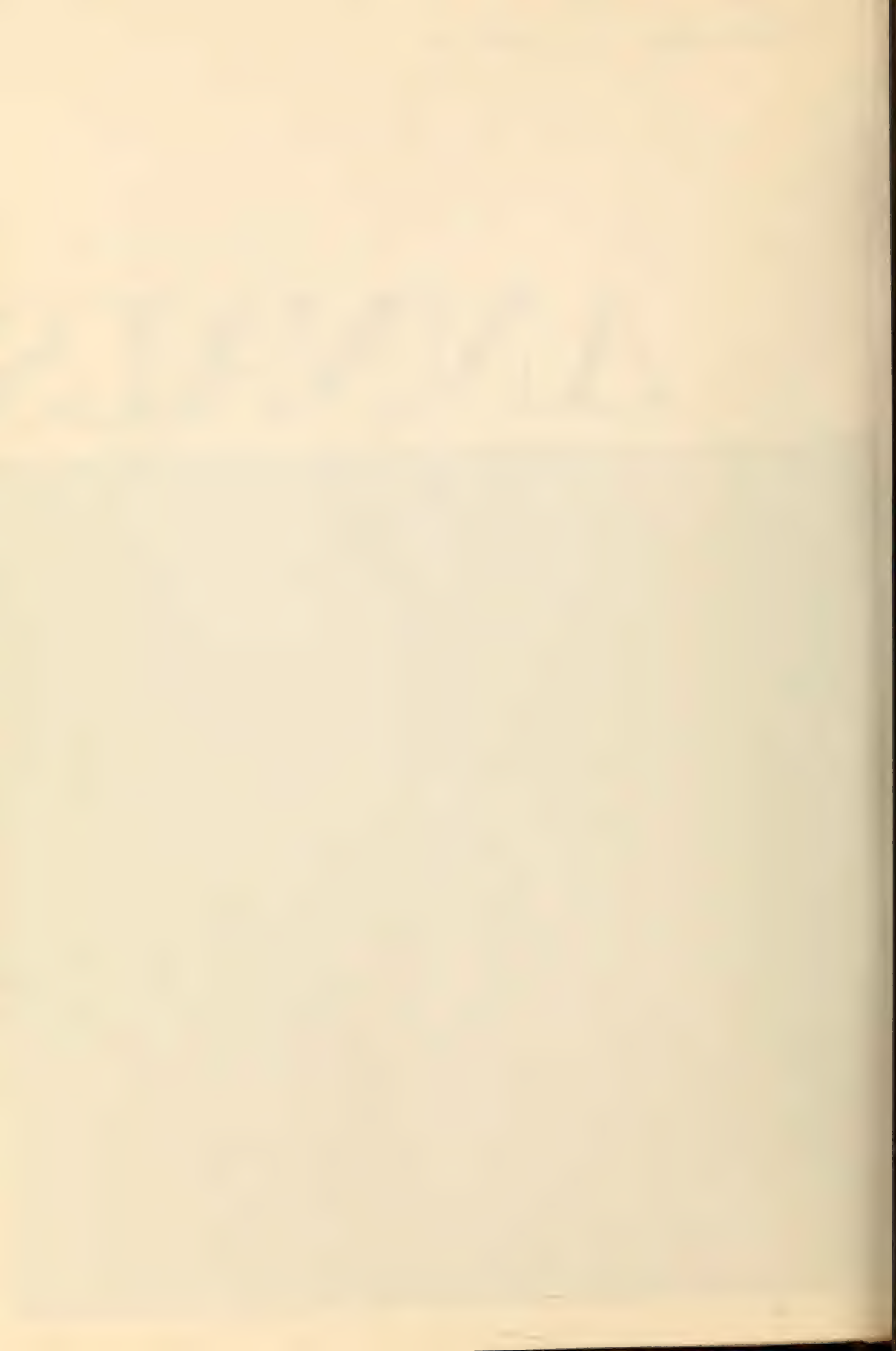
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THE AMPHIPODA OF SOUTHERN AFRICA
PART 4
THE GAMMARIDEA AND CAPRELLIDEA OF
THE CAPE PROVINCE EAST OF CAPE AGULHAS

By
C. L. GRIFFITHS

Cape Town Kaapstad

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C. L. GRIFFITHS

C.S.I.R. Oceanographic Research Unit, University of Cape Town

(With 18 figures)

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INTRODUCTION

This paper forms the fourth part of a series dealing with the gammaridean and caprellid amphipod fauna of Africa south of 20°S. Parts one to three (Griffiths 1973 and 1974*a* and *b*) have covered southern Moçambique, southern South West Africa and Natal respectively, while the present section deals with the Cape Province east of Cape Agulhas (i.e. from 20°E to 30°E).

A feature of this region is the considerable number of estuaries to be found there, many of which have been investigated by ecological survey teams from the University of Cape Town. However, most of these studies have been cursory and really only Knysna Estuary has been adequately worked on, resulting in a paper on its ecology by Day, Millard & Harrison (1952).

The marine sampling coverage for the eastern Cape, on the other hand, has been relatively thorough, over 700 marine samples being represented in the University of Cape Town collections (compared with 200 from Moçambique, 250 from South West Africa and 350 from Natal). An emphasis on the Cape is equally evident in the works of Stebbing (1908*a*, 1910*a*) and K. H. Barnard (1916, 1925, 1940, 1955) and this increased collecting effort has revealed a comparably larger haul of species (173, compared with 65, 81 and 115 from Moçambique, South West Africa and Natal respectively). At this stage it cannot be definitely stated whether the Cape fauna is richer than that of the other areas,

or whether the increased number of species is merely due to increased collecting effort. However, the amphipod faunas of temperate areas have, in general, been found to be richer than those of more tropical zones.

The dominant ocean current in the eastern Cape is the south-westerly flowing Agulhas Current, the inner margin of which tends to follow the continental shelf. At its centre the current flows at a rate of about three knots, but this decreases rapidly with depth. As the continental shelf widens towards the west the warm Agulhas water is progressively forced further offshore and inshore counter-currents and cold-water upwellings become progressively more important. Thus, while surface temperatures at the core of the Agulhas Current are usually in the range 20–25°C, thermoclines and upwellings mean that bottom temperatures are considerably lower. Over the Agulhas Bank itself a flow of upwelled water from south-east to north-west maintains the bottom temperature at 10–13°C. Slightly higher figures are obtained to the east of the bank, so that at Still Bay temperatures at 50 m fall around 15°C, dropping to 12°C at 200 m. As one progresses east there is a further rise so that at Port Elizabeth the temperature at 50 m averages about 17°C while north of East London a comparable figure would be 18–20°C. It must be stressed that the inshore regime is subject to considerable variation caused by periodic upwellings and counter-current intensities. For example, during periods of strong westerly winds the whole Agulhas Bank region becomes an Atlantic Ocean province, with a consequent drop in surface temperature.

As the collections of the University of Cape Town from the southern and eastern Cape Province fall into a large number of different sections these are discussed briefly below under the categories of collections from the open sea, and those from estuaries. The collecting locations are shown on Figure 1.

THE COLLECTING STATIONS

Collections from the marine environment

(a) Still Bay shelf transect (SST)

The samples in this series were collected off Still Bay on 20 to 22 June 1972 and form part of the material for an analysis of benthic distribution being undertaken by Dr J. G. Field of the C.S.I.R. Oceanographic Research Unit, University of Cape Town. The amphipod material derived from this collection has proved particularly diverse and interesting. A total of 66 species was recovered from the 82 samples, which were taken in the form of a transect from 5 to 200 m. These species included eight new to science, as well as a number of new records and rare species. The majority of these new species and new records was recovered from the 200 m station which appears to represent a habitat type not previously adequately sampled, since large numbers of new species from various other groups were also recovered here.

The transect was originally planned to sample an area of shelly sand, but

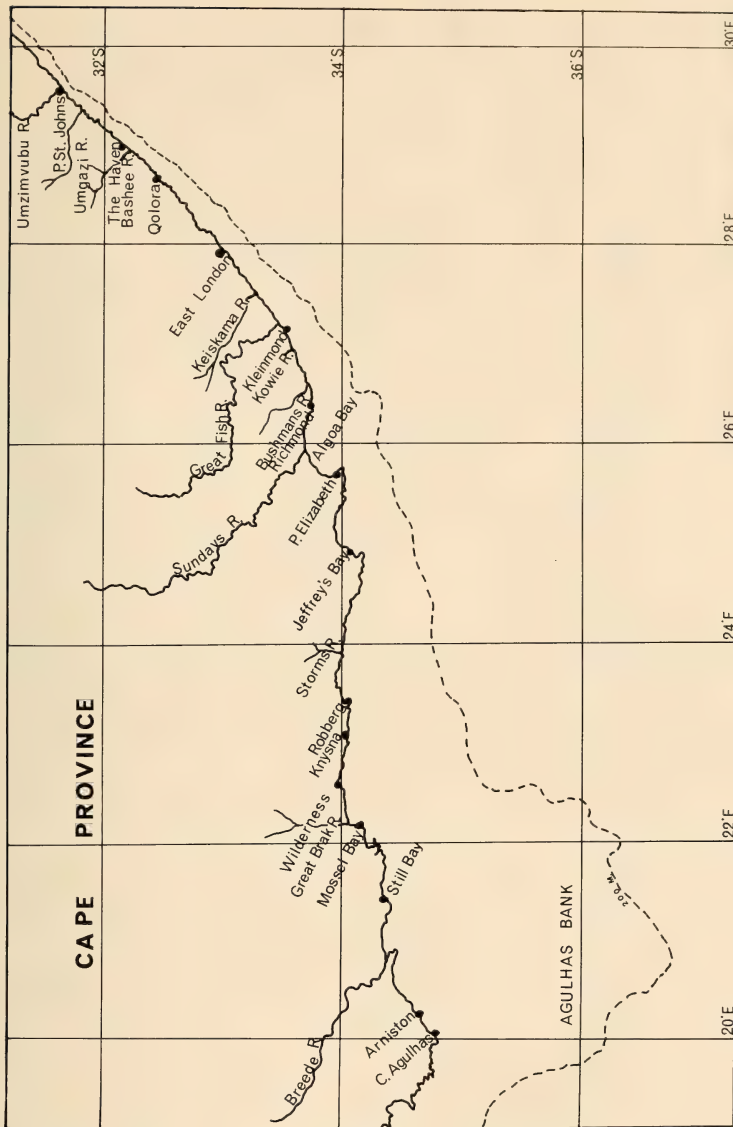


Fig. 1. The eastern Cape Province showing collecting areas referred to in the text.

a band of green mud was found to occupy a region from 50 to 80 m. The sandy area from 5 to 50 m was not heavily populated by amphipods, although *Urothoe pulchella*, *Mandibulophoxus stimpsoni*, *Hippomedon onconotus* and a few other species were reasonably common. The muddy zone from 50 to 80 m was very sparsely populated with just a few *Ampelisca brevicornis* and *Periculodes longimanus* and an occasional concentration of *Siphonoecetes dellavallei*. In the area deeper than 80 m a great diversity of species was to be found, the 200 m

station being particularly rich. Large *Ampelisca* were a feature of the area, notably *A. fusca*, but also *A. chiltoni* and *A. brevicornis*. *Mandibulophoxus stimpsoni* and *Leucothoe richiardi* were also well represented while the unusual *Concholestes armatus* n. sp. was discovered roaming the surface in old scaphopod shells.

SST station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>	<i>Depth (m)</i>	<i>Substrate</i>
SST 1-17	20/6/72	35°22'S/22°31'E	200	Rock and sand
SST 18-24	20/6/72	35°06'S/22°15'E	120	Shelly sand
SST 29-37	21/6/72	34°40'S/21°39'E	80	Shelly sand
SST 40-45	21/6/72	34°25'S/21°28'E	50	Green mud
SST 47-57	21/6/72	34°24'S/21°27'E	30	Shelly sand
SST 58-60	21/6/72	34°23'S/21°26'E	10	Shelly sand
SST 61-66	21/6/72	34°23'S/21°26'E	15	Shelly sand
SST 67-73	21/6/72	34°23'S/21°26'E	20	Shelly sand
SST 74-75	22/6/72	34°23'S/21°26'E	20	Shelly sand
SST 76	22/6/72	34°23'S/21°26'E	15	Shelly sand
SST 77	22/6/72	34°22'S/21°26'E	5	Shelly sand
SST 81	22/6/72	34°46'S/20°25'E	81	Green mud

(b) *Algoa Bay dredge (LIZ)*

This code has been allocated to a series of some 40 grab and dredge samples collected in Algoa Bay during April 1954. Eleven of these samples revealed amphipods, 24 species being represented. The only species at all common in the area were *Ampelisca chiltoni*, *Ampelisca diadema*, *Cheiriphotis megacheles* and the ubiquitous *Paramoera capensis*.

LIZ station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>	<i>Depth (m)</i>	<i>Substrate</i>
LIZ 1	5/4/54	33°55'S/25°37'E	8-10	Mud
LIZ 3	5/4/54	33°56'S/25°40'E	17-18	Sand
LIZ 13	6/4/54	33°58'S/25°38'E	7-8	Sand
LIZ 17	7/4/54	33°58'S/25°40'E	14	Stones
LIZ 19	7/4/54	33°58'S/25°42'E	27	Sand and shells
LIZ 25	11/4/54	34°00'S/25°44'E	39	Sand and shells
LIZ 29	11/4/54	34°00'S/25°42'E	5-7	Rock
LIZ 31	6/4/54	33°57'S/25°38'E	9	Limestone and clay
LIZ 32	6/4/54	33°58'S/25°39'E	9	Stones
LIZ 37	6/4/54	33°58'S/25°39'E	9	Stones
LIZ 40	11/4/54	34°00'S/25°42'E	7	Rock

(c) *Mossel Bay dredge (MB)*

The MB code is carried by a series of 88 dredge samples collected in Mossel Bay during January 1956. The substrate of the bay is predominantly sand, although there are considerable outcrops of rock. Twenty-four amphipod species are recorded from the area. Samples taken from rock showed the most frequently encountered species to be *Ceradocus rubromaculatus* and *Gammaropsis atlantica* as well as *Leucothoe* spp. and *Caprella* spp. Sandy areas contained

numerous *Cheiriphotis megacheles*, *Lysianassa ceratina* and *Ampelisca* spp., while *Paramoera capensis*, the most common species in the bay, was found in both rocky and sandy areas.

MB station data				
Catalogue No.	Date	Location	Depth (m)	Substrate
MB 4	12/1/56	34°09'S/22°07'E	10	Shell, rock
MB 5	12/1/56	34°08'S/22°08'E	21	Fine sand
MB 10	12/1/56	34°04'S/22°13'E	19	Rock
MB 13	12/1/56	34°04'S/22°13'E	19	Rock
MB 16	13/1/56	34°11'S/22°10'E	16	Sand and rock
MB 20	13/1/56	34°08'S/22°07'E	13	Sand, shells, rock
MB 21	13/1/56	34°10'S/22°08'E	8	Sand
MB 23	13/1/56	34°08'S/22°07'E	12,5	Rock
MB 28	13/1/56	34°11'S/22°09'E	19	Rock
MB 32	15/1/56	34°09'S/22°07'E	10	Shelly sand
MB 33	15/1/56	34°08'S/22°07'E	19	Sand
MB 34	15/1/56	34°08'S/22°09'E	31	Sand
MB 37	16/1/56	34°09'S/22°10'E	31	Sand
MB 38	16/1/56	34°10'S/22°07'E	8,5	Sand
MB 40	16/1/56	34°10'S/22°08'E	9	Rock
MB 41	16/1/56	34°10'S/22°08'E	9	Rock
MB 45	17/1/56	34°10'S/22°09'E	17	Sand
MB 46	17/1/56	34°11'S/22°10'E	26	Sand
MB 50	17/1/56	34°11'S/22°09'E	10	Rock
MB 54	17/1/56	34°10'S/22°09'E	14	Rock, sandy patches
MB 57	17/1/56	34°10'S/22°09'E	9	Rock
MB 58	18/1/56	34°04'S/22°13'E	12,5	Rock
MB 59	18/1/56	34°04'S/22°13'E	11,5	Rock
MB 61	18/1/56	34°04'S/22°14'E	17-20	Coarse sand, shell, rock
MB 66	18/1/56	34°04'S/22°13'E	26	Sand and rock
MB 69	19/1/56	34°08'S/22°07'E	13,5	Sand, rocky
MB 70	19/1/56	34°08'S/22°07'E	18	Sand
MB 71	19/1/56	34°08'S/22°07'E	12	Sand
MB 73	19/1/56	34°09'S/22°07'E	12	Rock, sand, shell
MB 75	19/1/56	34°08'S/22°07'E	15,5	Sand
MB 77	20/1/56	34°11'S/22°06'E	24	Rock and sand patches
MB 80	20/1/56	34°05'S/22°11'E	20,5	Fine sand and mud
MB 82	20/1/56	34°10'S/22°09'E	—	(Plankton haul)
MB 84	21/1/56	34°11'S/22°10'E	29	Rock
MB 86	17/1/56	34°11'S/22°09'E	10	Rock
MB 87	17/1/56	34°10'S/22°09'E	14	Rock, sandy patches.

(d) Trawler stations (TRA)

Material collected during excursions by members of the Zoology Department of the University of Cape Town on commercial trawlers are grouped under this code. Although there are 44 TRA stations in the area under consideration only three contain amphipods. Five species have been identified from these samples, none of them at all common.

TRA station data				
Catalogue No.	Date	Location	Depth (m)	Substrate
TRA 54	28/11/52	34°40'S/21°35'E	75	Rock
TRA 55	28/11/52	34°40'S/21°35'E	75	Rock
TRA 58	26/11/52	34°28'S/21°45'E	70	Sand and stones

(e) *South coast dredge (SCD)*

Grab and dredge samples collected between 20°E and 30°E along the southern Cape coast, and which do not form part of the specific studies mentioned above, are allocated to the SCD catalogue. To date there are some 400 samples in the series and included in the recorded fauna are 96 species of amphipod. Of these species *Mandibulophoxus stimpsoni* and *Perioculodes longimanus* have been the most commonly found, while other frequently occurring species have been *Ampelisca brevicornis*, *Ampelisca palmata*, *Aora typica*, *Cheiriphotis megacheles*, *Gammaropsis atlantica* and *Photis* and *Urothoe* spp.

SCD station data				
Catalogue No.	Date	Location	Depth (m)	Substrate
SCD 3	18/4/58	34°31'S/24°40'E	102	Rock
SCD 10	19/4/58	34°15'S/25°05'E	11	Rock and shell
SCD 20	26/5/58	34°07'S/23°23'E	46	Rock
SCD 24	26/5/58	34°46'S/23°27'E	110	Rock
SCD 34	21/5/58	33°03'S/27°56'E	57	Sand, shells
SCD 41	19/5/58	32°15'S/28°57'E	47	Rock
SCD 55	20/8/58	34°01'S/25°45'E	46	Rock
SCD 59	19/8/58	33°37'S/26°56'E	46	—
SCD 60	16/8/58	33°02'S/27°56'E	46	Rock
SCD 62	15/8/58	32°17'S/28°54'E	46	Rock
SCD 64	14/8/58	31°37'S/29°36'E	36,5	Mud
SCD 74	16/7/59	32°33'S/28°38'E	55	Sand and mud
SCD 81	16/7/59	32°43'S/28°28'E	58	Stones, shells
SCD 83	17/7/59	27°54'S/33°03'E	51	Sand, shells
SCD 93	17/7/59	33°03'S/27°55'E	27	Rock
SCD 94-96	20/7/59	34°21'S/25°41'E	110	Shell
SCD 99	21/7/59	34°33'S/24°01'E	130	Rock
SCD 100	21/7/59	34°33'S/24°01'E	130	Rock
SCD 102	21/7/59	34°33'S/24°01'E	130	Rock
SCD 103	22/7/59	35°07'S/22°15'E	120	Sand
SCD 104-5	23/7/59	34°33'S/21°28'E	67	Sand, shells
SCD 106	23/7/59	34°35'S/21°10'E	67	Rock
SCD 110	23/7/59	34°35'S/21°11'E	75	Sand, stones
SCD 115	26/11/59	34°54'S/22°12'E	106	Sand, shells
SCD 118	14/2/60	34°24'S/21°46'E	18	Rock
SCD 120	14/2/60	34°33'S/21°52'E	77	Sand
SCD 122	14/2/60	34°40'S/22°00'E	93	Sand
SCD 124	3/6/60	34°26'S/21°48'E	67	Mud
SCD 127-8	3/6/60	34°37'S/21°56'E	87	Sand
SCD 131	3/6/60	34°48'S/22°06'E	100	Sand
SCD 135	26/11/59	34°29'S/21°49'E	73	Mud
SCD 138	28/8/60	34°35'S/21°56'E	77	Shells
SCD 141	28/8/60	34°46'S/22°05'E	93	Sand
SCD 146	28/8/60	34°46'S/22°05'E	93	Sand
SCD 148	28/8/60	34°59'S/22°18'E	106	Sand
SCD 151	2/6/60	34°55'S/21°26'E	91	—
SCD 159	25/11/60	34°03'S/25°59'E	84	Rock
SCD 160	25/11/60	34°03'S/25°59'E	84	Rock
SCD 172	24/11/60	33°58'S/25°41'E	4-11	Rock
SCD 179	24/11/60	33°58'S/25°41'E	4-11	Rock
SCD 181	30/11/60	34°20'S/23°31'E	110	Sand
SCD 184	25/11/60	34°23'S/26°01'E	137	Sand, shells

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>	<i>Depth (m)</i>	<i>Substrate</i>
SCD 185	25/11/60	34°13'S/26°04'E	124	Sand
SCD 188	30/11/60	34°10'S/23°32'E	97	Mud
SCD 189	29/11/60	34°05'S/23°23'E	10	Sand
SCD 192-3	29/11/60	34°04'S/23°25'E	47	Mud
SCD 194	29/11/60	34°04'S/23°25'E	43	Sand
SCD 198	29/11/60	34°07'S/23°31'E	79	Sand
SCD 199	30/11/60	34°10'S/23°32'E	97	Mud
SCD 202	29/11/60	34°05'S/23°23'E	10	Sand
SCD 204	30/11/60	34°51'S/23°41'E	183	Sand
SCD 208	25/11/60	34°23'S/26°01'E	137	Sand, shells
SCD 211	24/11/60	33°58'S/25°42'E	26	Sand, shells
SCD 216	25/11/60	34°03'S/25°58'E	78	Sand, shells
SCD 219	29/11/60	34°02'S/23°28'E	49	Rock
SCD 222	25/11/60	34°13'S/26°04'E	124	Sand
SCD 225	30/11/60	34°20'S/23°31'E	112	Rock
SCD 227	29/11/60	34°07'S/23°31'E	79	Sand
SCD 228	5/12/60	35°43'S/20°31'E	143	Mud
SCD 230	29/11/60	34°04'S/23°25'E	43	Sand
SCD 232	4/12/60	36°28'S/21°11'E	183	Sand
SCD 235-7	30/11/60	34°51'S/23°41'E	183	Sand
SCD 244-5	29/11/60	34°02'S/23°28'E	49	Rock
SCD 248	29/11/60	34°04'S/23°25'E	45	Mud
SCD 249	30/11/60	34°48'S/23°39'E	148	Rock
SCD 253	16/7/61	33°07'S/28°01'E	88	Rock
SCD 257	14/7/61	33°53'S/25°42'E	32	Sand
SCD 262	14/7/61	33°48'S/25°47'E	27	Rock
SCD 267	16/7/61	33°02'S/27°56'E	55	Sand, rock
SCD 269	19/7/61	34°23'S/25°54'E	182	Sand, shells
SCD 273	19/7/61	34°23'S/25°54'E	182	Sand, shells
SCD 276	14/7/61	33°53'S/25°42'E	32	Sand
SCD 278	16/7/61	33°02'S/27°56'E	55	Sand, rock
SCD 280	16/7/61	33°09'S/28°05'E	274	Rock
SCD 282-3	11/2/62	34°04'S/23°23'E	22	Sand, shells
SCD 285	6/2/62	33°01'S/27°55'E	7	Sand
SCD 286	6/2/62	33°01'S/27°55'E	7	Sand
SCD 287	11/2/62	34°04'S/23°23'E	22	Sand, shells
SCD 288	6/2/62	33°04'S/27°57'E	84	Shells
SCD 295	6/2/62	33°04'S/27°57'E	84	Shells
SCD 300	6/2/62	33°09'S/28°02'E	84	—
SCD 302	6/2/62	33°39'S/27°15'E	88	Sand
SCD 304	8/2/62	34°00'S/25°53'E	46	Rock
SCD 308	8/2/62	34°00'S/25°53'E	46	Rock
SCD 310	9/2/62	33°59'S/25°51'E	50	Mud
SCD 311	9/2/62	33°59'S/25°51'E	50	Mud
SCD 312	9/2/62	33°58'S/25°47'E	48	Sand
SCD 315	9/2/62	33°58'S/25°47'E	48	Sand
SCD 319	9/2/62	34°15'S/25°50'E	108	Sand, rock
SCD 321	9/2/62	34°15'S/25°50'E	108	Sand, rock
SCD 324	9/2/62	34°27'S/25°57'E	172	Sand
SCD 326	9/2/62	34°27'S/25°57'E	172	Sand
SCD 328	10/2/62	34°43'S/25°40'E	—	(Glass buoy)
SCD 329	11/2/62	34°04'S/23°23'E	22	Shell
SCD 332	11/2/62	34°03'S/23°23'E	11-18	Sand
SCD 338	11/2/62	34°02'S/23°27'E	42	Mud
SCD 339	11/2/62	34°02'S/23°27'E	42	Mud
SCD 342	11/2/62	34°39'S/23°41'E	121	Shell, sand
SCD 343	11/2/62	34°39'S/23°41'E	121	Sand, shells

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>	<i>Depth (m)</i>	<i>Substrate</i>
SCD 345	12/2/62	34°16'S/22°17'E	73	Sand, mud
SCD 347	12/2/62	34°10'S/22°15'E	54	Mud
SCD 348	12/2/62	34°09'S/22°10'E	36	Sand
SCD 349	12/2/62	34°09'S/22°09'E	18	Sand
SCD 350	13/2/62	34°28'S/21°50'E	73	Sand
SCD 352	16/4/62	34°25'S/25°56'E	210	Mud, shells
SCD 353	6/2/62	33°04'S/27°57'E	84	Sand, shells
SCD 356	6/11/62	36°01'S/19°45'E	300	Sand, mud
SCD 359	19/11/62	34°48'S/22°51'E	120	—
SCD 366	2/12/62	33°50'S/25°47'E	36	Sand, rock
SCD 368	2/12/62	33°50'S/25°47'E	36	Sand
SCD 370	4/12/62	33°59'S/25°45'E	44	Sand
SCD 373	4/12/62	33°59'S/25°51'E	36-54	Sand, shells
SCD 374	4/12/62	33°59'S/25°51'E	54	Sand, shells
SCD 376	4/12/62	33°53'S/25°49'E	44	Sand
SCD 379	5/12/62	33°53'S/25°48'E	44	Sand
SCD 381	5/12/62	33°53'S/25°48'E	44	Sand
SCD 383	5/12/62	33°52'S/25°38'E	7	Sand
SCD 384	5/12/62	33°52'S/25°38'E	7	Sand
SCD 388	8/12/62	34°04'S/23°23'E	46	Rock
SCD 391	8/12/62	34°05'S/23°23'E	11	Sand
SCD 392	9/12/62	35°08'S/22°02'E	125	Sand, shells

(f) *Shore stations*

The collections falling into this group are the earliest made by the University of Cape Town Ecological Survey and were intended to reveal zonation of the intertidal fauna around the South African coast. The various collections are denoted by the following catalogue codes (most of the stations were visited only once, but where material was collected on subsequent visits this is indicated by doubling the code letter for second visits and tripling it in the case of third visits).

<i>Catalogue code</i>	<i>Location</i>	<i>Map reference</i>
J	Port St. Johns	31°38'S/29°33'E
H	The Haven	32°14'S/28°55'E
Q	Qolora	32°38'S/28°26'E
L, LL, LLL	East London	33°02'S/27°54'E
X	Kleinmont	33°33'S/27°04'E
K	Kowie	33°36'S/26°54'E
Y	Richmond	33°44'S/26°35'E
E	Port Elizabeth	33°58'S/25°38'E
Z, ZZ	Jeffreys Bay	34°05'S/24°55'E
T	Storms River	34°02'S/23°54'E
R, RR	Robberg	34°05'S/23°22'E
KN, KKN	Knysna	34°05'S/23°04'E
V, VV	Mossel Bay shore	34°11'S/22°09'E
S, SS	Still Bay shore	34°23'S/21°26'E
AR	Arniston	34°41'S/20°14'E
AG	Cape Agulhas	34°50'S/20°10'E

Amphipod records at these locations are purely of a presence-absence type, since the original purpose of the collections was to give an indication of distribution.

Species most frequently encountered intertidally in this area are *Ceradocus rubromaculatus*, *Hyale grandicornis*, *Jassa falcata*, *Lysianassa ceratina* and *Paramoera capensis*, which were found at virtually all the collecting stations. A number of species appear to be restricted to the intertidal zone and have yet to be found sublittorally. These include *Ampithoe africana*, *Elasmopus pectenicrus*, *Palinotus natalensis*, *Temnophlias capensis* and *Hyale* and *Talorchestia* spp.

Collections from estuaries

(a) *Estuaries near Port St. Johns (STJ)*

The largest of the rivers in this area is the Umzimvubu, which enters the sea at the town of Port St. Johns. At the time of sampling (1950) the estuary was muddy but became sandy near the mouth. Heavy silting had restricted the fauna but *Grandidierella bonnieroides* and *G. chelata* were abundant among stones near the mouth while *G. lingorum* was dominant further upstream. *Melita zeylanica* and *Orchestia rectipalma* were also to be found on the mud flats, while *Talorchestia* and *Orchestia* spp. occupied the driftline. *Urothoe pulchella* was also recovered, but was restricted to clean sand near the mouth.

Just south of the town of Port St. Johns lie two minor estuaries known as the Eastern and Western Estuaries. Here again muddy zones were occupied by such typical estuarine species as *Melita zeylanica*, *Corophium triaenonyx* and *Grandidierella* spp. while *Urothoe pulchella* was to be found in clean sand.

The Umgazi Estuary, a few kilometres further south, was also sampled. Here again the fauna conformed to the pattern typical of the area with *Melita zeylanica*, *Corophium triaenonyx* and *Grandidierella* spp. giving way to *Afrochiltonia capensis* further upstream.

A brief exploratory visit to the Umgazana River 6 km south of the Umgazi revealed a population of *Orchestia rectipalma* living amongst algae on the pneumatophores of mangroves.

STJ station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
STJ 5	17/1/50	Drift line, Umzimvubu R. mouth
STJ 6	17/1/50	Intertidal mud, Umzimvubu R. mouth
STJ 7	17/1/50	Rocks, Umzimvubu R. mouth
STJ 8	17/1/50	Mud sievings, Umzimvubu R. mouth
STJ 14	18/1/50	Clean sand, Umzimvubu R. mouth
STJ 15	18/1/50	Clean sand, Umzimvubu R. mouth
STJ 16	18/1/50	Western Estuary
STJ 17	18/1/50	Mouth of Eastern Estuary
STJ 18	18/1/50	Mud bank, 2 km up Umzimvubu R.
STJ 24	19/1/50	Netting, 2 km up Umgazi R.
STJ 26	19/1/50	Muddy sand, 2 km up Umgazi R.
STJ 27	19/1/50	Under stones, Umgazi R. mouth
STJ 28	19/1/50	Mangrove roots, Umgazana R.
STJ 29	19/1/50	Sandy beach, Umgazi R. mouth
STJ 31	20/1/50	Decaying wood, Western Estuary
STJ 32	20/1/50	Weeds and stones, Western Estuary

(b) *Estuaries near The Haven hotel (HAV)*

Three estuaries in the vicinity of The Haven were briefly visited by a party of biologists from the University of Cape Town in January 1950.

The Bashee River winds across a narrow flood plain bordered by steep wooded hills and then widens into a lagoon before entering the sea between sand dunes. The area near the mouth is predominantly sandy but there are occasional rocky outcrops, further upstream the sand is replaced by mud and there is a dense growth of reeds and patches of mangroves. The muddy zones were dominated by *Grandidierella lignorum* while the clean sand near the mouth was occupied by *Urothoe pulchella*. *Orchestia ancheidos* occurred along the drift line.

Blind Lagoon is a small, almost permanently closed estuary just below the hotel. At the seaward end the bottom is sand but this is replaced upstream by mud which forms the bottom of the rest of the lagoon except the head, where there are outcrops of rock. The body of the estuary was well colonized by seven species of amphipod, all typical estuarine forms. Most common of these was *Grandidierella chelata* which was originally described from specimens collected here.

The Mpanyana River Estuary consists of a large lagoon surrounded by steep wooded banks and flowing into the sea through a narrow sandy channel. At the time of sampling the depth of the lagoon was less than 30 cm and the bottom graduated from sand at the seaward end through mud to stones at the head. Near the outlet *Corophium triaenonyx*, *Grandidierella lignorum* and *Urothoe pulchella* were common while further upstream they were replaced by *Melita zeylanica* and *Orchestia rectipalma*.

HAV station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
HAV 3	12/1/50	Outlet of Mpanyana R.
HAV 5	13/1/50	Sand, Blind Lagoon
HAV 7	13/1/50	D-netting, Blind Lagoon
HAV 8	13/1/50	Submerged log, Blind Lagoon
HAV 9	13/1/50	Rocks, Blind Lagoon
HAV 10	13/1/50	Stones, Blind Lagoon
HAV 13	13/1/50	D-netting, mouth of Bashee R.
HAV 17	14/1/50	Sand, mouth of Mpanyana R.
HAV 18	14/1/50	Stones, 1 km up Mpanyana R.
HAV 20	14/1/50	Netting, 4 km up Bashee R.

(c) *Keiskama Estuary (HAM)*

The Keiskama River is tidal for some 30 km, widening over this distance to some 2 km at Hamburg before entering the sea between headlands at 33°18'S/27°29'E. The river carries a good deal of silt and is shallow and muddy except at the actual mouth where there are rocks and a small area of clean sand. Only five species of amphipod have been recovered from the system. Of these *Orchestia ancheidos* and *Talorchestia capensis* were locally common under

weeds along the driftline, while *Afrochiltonia capensis*, *Melita zeylanica* and *Orchestia rectipalma* were to be found under stones and among weeds throughout the tidal reaches.

HAM station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
HAM 3	9/1/50	<i>Zostera</i> bed, 1 km from mouth
HAM 4	9/1/50	Driftline, 1 km from mouth
HAM 9	10/1/50	Under stones, Hamburg jetty
HAM 11	10/1/50	Hand netting, 8 km from mouth
HAM 13	11/1/50	Hand netting, 30 km from mouth

(d) *Bushmans River* (BMR)

A brief examination of the Bushmans River Estuary by a team from the Zoology Department of the University of Cape Town in September 1950 revealed five amphipod species. The upper reaches were colonized by a typical fauna of *Grandidierella lignorum*, *Corophium triaenonyx* and *Melita zeylanica* with *Orchestia ancheidos* occurring along the banks. The only unusual record was one of *Ampelisca spinimana* from *Zostera* near the mouth (33°41'S/26°41'E).

BMR station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
BMR 7	9/9/50	Digging and netting 30 km from mouth
BMR 21	12/9/50	Bank, 24 km from mouth
BMR 23	14/9/50	<i>Zostera</i> bed, 4 km from mouth
BMR 25	14/9/50	Reed bed, 40 km from mouth
BMR 26	15/9/50	<i>Zostera</i> bed, 4 km from mouth

(e) *Sundays River Estuary* (SUN)

The Sundays River flows between vertical mudbanks until about 1 km from the wide shallow mouth (at 33°43'S/25°51'E) where the bottom becomes sandy and the east bank rocky. A survey of the fauna revealed only three amphipod species. Of these *Urothoe pulchella* and *Corophium triaenonyx* were recovered from clean sand near the mouth, while *Melita zeylanica* occurred amongst weeds on the piles of a bridge 8 km upstream.

SUN station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
SUN 5	7/1/50	D-netting, sand flats at mouth
SUN 6	7/1/50	General collection, 8 km from mouth

(f) *Knysna Estuary* (KNY)

The Knysna Estuary is the richest in southern Africa and has been the subject of a detailed report by Day, Millard & Harrison (1952), who describe the topography and fauna of the system, based upon expeditions to the area between 1947 and 1955. These records have since been supplemented by a further collection taken in 1964.

The Knysna River lies 80 km east of Mossel Bay and widens into a large tidal basin over the last 18 km before entering the sea between two massive headlands at 34°05'S/23°04'E. The estuary is S-shaped and can be regarded as beginning at Charlesford Rapids. Below the rapids lies a stony ford known as 'The Old Drift'. From this point the river winds between marshy banks and beneath the Westford road bridge and then widens abruptly. Around the banks of the muddy upper basin lie the areas of Eastford, Ashford, Belvedere and The Point, while the small Salt River enters the north bank just above the railway bridge. Below the bridge the estuary is over 3 km wide and the channel is fringed by extensive muddy banks covered in *Zostera*. There are two islands in the lower basin, the upper of these, Paarden Island, lies just off Knysna town and on it is situated Thesen's wharf. The lower island, Leisure Island, is connected to the mainland by a causeway crossing boggy salt marshes. Below Leisure Island the lagoon narrows, the channel rapidly deepens and the banks become rocky before entering the heads at Fountain Point.

The flow in the estuary is generally not strong but is sufficient to maintain a salinity gradient. Tidal range at the heads is about 2 m, this range is maintained as far as Westford bridge but falls to 0,3 m at Charlesford. Within the lagoon wave action is negligible despite the vicious waves pounding the heads. Salinity only begins to fall significantly above the rail bridge at which point values of about 30‰ are usual (although there may be significant layering effects). At Westford bridge salinity ranges from 15–25‰ while comparable figures at Charlesford are 3–7‰.

Twenty-seven species of amphipod have been found in Knysna Estuary. Most of these are not typical estuarine forms and are restricted to the area below the railway bridge where salinity remains high. Most widespread in this area are *Cymadusa filosa*, which lives in mucous tubes on *Zostera* plants, and *Paramoera capensis*, *Jassa falcata*, *Corophium triaenonyx* and *Lembos hypacanthus*, which are locally abundant, especially on hard surfaces. Above the railway bridge the amphipod fauna is dominated by estuarine species such as *Grandidierella lignorum*, *Melita zeylanica*, *Orchestia rectipalma* and *Corophium triaenonyx* which all extend as far as Charlesford Rapids.

KNY station data

Catalogue No.	Date	Location
KNY 6	15/4/47	Dredge below Paarden Island
KNY 11	16/7/47	Dredge below Paarden Island
KNY 13	15/7/47	Channel west of Leisure Isle
KNY 28	17/7/47	Channel, Leisure Isle
KNY 30	16/7/47	Channel off Thesen's wharf
KNY 42	18/7/47	<i>Zostera</i> bed, Salt River
KNY 43	17/7/47	<i>Zostera</i> bed, Leisure Isle
KNY 50	19/7/47	Westford bridge
KNY 57	20/7/47	Channel at Fountain Point
KNY 81	27/11/47	Belvedere
KNY 101	12/4/49	Below Charlesford
KNY 103	—/4/49	Westford bridge

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
KNY 112	14/4/49	Below Charlesford
KNY 113	14/4/49	<i>Zostera</i> bed, 'The Point'
KNY 114	14/4/49	<i>Zostera</i> bed, Leisure Isle
KNY 122	12/4/49	Westford bridge
KNY 128	14/4/49	Causeway below Woodbourne
KNY 139	12/4/49	<i>Zostera</i> bed, Paarden Island
KNY 157	27/3/50	Seaward side of Leisure Isle
KNY 160	—/11/47	Charlesford Rapids
KNY 162	9/7/50	Rail bridge
KNY 166	9/7/50	Leisure Isle and buoys in channel
KNY 171	9/7/50	Knysna Heads and Fountain Point
KNY 175	10/7/50	Charlesford Rapids
KNY 176	11/7/50	Buoy off Leisure Isle
KNY 179	11/7/50	Sandbank at Brenton
KNY 181	12/7/50	Old drift
KNY 184	12/7/50	Charlesford
KNY 187	13/7/50	Sandbanks, Leisure Isle
KNY 191	14/7/50	Fountain Point
KNY 245	14/2/64	Leisure Isle
KNY 266	14/2/64	Ashford
KNY 272	15/2/64	Rail bridge
KNY 273	15/2/64	Rail bridge
KNY 274	15/2/64	Rail bridge
KNY 283	15/2/64	Rail bridge
KNY 285	15/2/64	Old Drift
KNY 286	15/2/64	Old Drift
KNY 291	15/2/64	Old Drift
KNY 294	14/2/64	Ashford

(g) *Estuaries near the Great Brak River (GBR)*

Three estuaries in the vicinity of the Great Brak River (34°03'S/22°14'E) were visited by the University of Cape Town Zoological Survey team in 1950. The amphipod faunas of the three rivers conform to the pattern typical of the area with *Urothoe pulchella* being found in clean sand near the mouth, while *Corophium triaenonyx*, *Melita zeylanica* and *Grandidierella lignorum* occurred throughout the estuaries. *Talorchestia australis* was found along the drift line.

GBR station data

<i>Catalogue No.</i>	<i>Date</i>	<i>Location</i>
GBR 12	30/4/50	Sand at mouth of Great Brak R.
GBR 13	30/4/50	Rocky shore near mouth, Great Brak R.
GBR 16	1/5/50	Sandy bottom of Great Brak R. 1 km from mouth
GBR 23	2/5/50	Above road bridge, Little Brak R.
GBR 24	2/5/50	Head of estuary, Little Brak R.
GBR 37	3/5/50	Weeds at mouth, Great Brak R.
GBR 46	4/5/50	Mouth of Wilderness Estuary

(h) *Breede River Estuary (BRE)*

The Breede River is one of the largest in the Cape Province and has been the subject of two expeditions by the University of Cape Town Ecological Survey. Over the last 50 km of its course the river is tidal and the channel reaches 8 m in depth. The mouth (at 34°25'S/20°53'E) is permanently open with

a sand spit and rocky areas to the north, while the southern shore displays extensive mud and sand flats. At Karools Kraal, situated 7 km from the mouth, the river is narrow and deep and runs between rocky banks interspersed with muddy bays in which there are *Zostera* beds. Below this point the river flows past Dolla se Baai and Green Point to Moddergat where the *Zostera* becomes more extensive. Port Beaufort lies on the north bank about 2 km from the mouth and Low Tide estate is opposite it on the south bank.

From this point to Witsands at the mouth the banks are mostly sand which is locally muddy and covered with a luxuriant growth of *Zostera* at the lower levels. At the mouth itself the south bank consists of wave-washed rocks which display a true marine fauna.

Six species of amphipod have been found in the estuary. Of these *Lysianassa ceratina* occurred only at the mouth and not under estuarine conditions. *Melita zeylanica* and *Orchestia rectipalma* were found throughout the system while *Grandidierella lignorum* was common amongst *Zostera* and *Talorchestia capensis* along the drift line. *Paramoera capensis* was found in the Low Tide estate area.

BRE station data

Catalogue No.	Date	Location
BRE 5	1/7/51	Drift line, Port Beaufort
BRE 13	2/7/51	<i>Zostera</i> bed, Moddergat
BRE 18	2/7/51	Drift line, Moddergat
BRE 30	3/7/51	Between Witsands and Port Beaufort
BRE 31	3/7/51	Between Witsands and Port Beaufort
BRE 34	4/7/51	Intertidal rocks, Port Beaufort
BRE 43	4/7/51	Rocks, Karools Kraal
BRE 44	5/7/51	Rocks at mouth
BRE 51	6/7/51	<i>Zostera</i> bed, Green Point
BRE 52	6/7/51	<i>Zostera</i> bed, Moddergat
BRE 55	6/7/51	Karools Kraal
BRE 56	6/7/51	Karools Kraal
BRE 57	6/7/51	Karools Kraal
BRE 71	8/7/51	<i>Zostera</i> bed, Green Point
BRE 77	8/7/51	<i>Zostera</i> bed, Dolla se Baai
BRE 81	8/7/51	From stomach of <i>Lithognathus</i>
BRE 123	5/2/52	Karools Kraal
BRE 128	5/2/52	Under stones, Karools Kraal
BRE 135	6/2/52	Among weeds, Low Tide estate
BRE 144	7/2/52	Rocks at mouth
BRE 146	8/2/52	Karools Kraal

SYSTEMATICS

Taxonomy of the Gammaridea followed here is that adopted by J. L. Barnard (1969b) and amended by J. L. Barnard (1970, 1972b), while that of the Caprellidea is modelled on the system proposed by McCain (1970). The arrangement of families, genera within each family and then of species within each genus is alphabetic. Limbs of the pereon are referred to as gnathopods 1 and 2 followed by pereopods 1–5 (while most authors use this system some number the pereopods according to the segments on which they occur, i.e. gnathopods 1 and 2 followed by pereopods 3–7). The analysis presented here is restricted

to species occurring between the drift line and 1 000 m depth, thus estuarine and beach-living species are included, while terrestrial and freshwater forms are excluded, as are those found only at abyssal depths. Holotypes of all new species have been placed in the South African Museum, Cape Town, paratypes have been retained by the University of Cape Town.

For each species at least one reference has been given to what is considered an accurate and, if possible, well-illustrated description. Full synonymies and reference lists may be found through these descriptions. Where diagnoses are provided they are intended to distinguish the species from others in the genus. Generic and familial diagnoses are to be found in J. L. Barnard (1969*b*), or may be located through McCain & Steinberg (1970), in the case of the Caprellidea.

The sample coding system used here is that employed by the University of Cape Town. Each area has its own catalogue indicated by a code of one, two or usually three letters (MB = Mossel Bay, KNY = Knysna, etc.). Each sample from that area is numbered and then each species within the sample is denoted by a letter of the alphabet. Thus each specimen bears a catalogue/-sample/species code. For example a sample from Mossel Bay is allocated to the MB catalogue. The first sample in this catalogue is MB 1 and the species from that sample called MB 1A, MB 1B, MB 1C, etc. Where the number of individual specimens is recorded this is indicated by a figure following the code in brackets. Thus MB 1D(6) indicates that six specimens of the species D were collected from station number 1 in the Mossel Bay series.

Authors working in this area in the past frequently gave collecting locations in a somewhat vague manner, e.g. 'Off Cape Agulhas' or '5 miles SE of Cape Infanta'. In presenting these records I have given the latitude/longitude square in which they were made, followed by the depth and the reference from which the records were taken. Thus 33°S/28°E/47m (Stebbing 1917) indicates that Stebbing (1917) records the species in question from the 33°S/28°E area at a depth of 47 m. In some cases material reported on by K. H. Barnard (1951, 1955, 1957) was derived from University of Cape Town collections and in these cases only the University code is given.

Suborder GAMMARIDEA

Family Acanthonotozomatidae

Cypsiphimidia gibba K. H. Barnard, 1955

Cypsiphimidia gibba K. H. Barnard, 1955: 88, fig. 43.

Records: LIZ 40G(1).

Diagnosis: Pereon segment 1 swollen, its front margin nearly horizontal such that the head projects vertically downwards; coxa 1 partially concealed by 2; body entirely smooth; gnathopod 1 minutely chelate; gnathopod 2 subchelate; telson short, apically incised.

Distribution: The above record is the only one to date.

Dikwa n. gen.

Diagnosis: Upper lip slightly emarginate; mandible short and broad, with an acute apex, spine row and large molar; lobes of lower lip not incised; palp of maxilla 1 bi-articulate, exceeding outer plate; maxillipedal palp 4-articulate, exceeding outer plate, article 2 of palp not produced; gnathopod 1 chelate; gnathopod 2 simple; telson emarginate.

Type species: *Dikwa acrania* n. sp.

Relationships: The combination of chelate gnathopod 1 and simple gnathopod 2, together with the unusual mandible, demands the erection of this new genus.

Dikwa acrania n. sp.

Fig. 2

Description of female (3 mm): Head greatly reduced, shorter than first pereon segment and consisting largely of a rounded downturned rostrum (Fig. 2A), eyes absent; upper lip emarginate; mandible (Fig. 2C) short and broad with a 3-articulate palp, articles 1 and 2 of palp subequal, their surfaces markedly ridged, article 3 of palp the longest, a row of 14 strong setae along its medial margin, incisor consisting of a sharp projection, lacinia mobilis apically bifurcate, spine row of 13 strong spines, molar fairly large; lower lip not incised; maxilla 1 with bi-articulate palp exceeding outer plate, its distal margin setose, outer plate terminating in eight strong serrate spines, inner plate bearing three terminal setae; maxilliped with 4-articulate palp exceeding outer plate, none of the articles distally produced, outer plate bearing a distal row of eight plumose setae and a few simple setae, inner plate bearing a marginal and three sub-marginal rows of minute pectinations; antennae subequal, slightly shorter than pereon; article 1 of antenna 1 twice as wide as article 2 and as long as 2 and 3 together, apically lobed to partially envelop article 2, flagellum 14-articulate, accessory flagellum absent; flagellum of antenna 2 15-articulate.

Coxae complex (Fig. 2A) but generally very thick and acuminate, coxa 7 very elongate and distally produced into an acute backwardly curved tooth; pereon dorsally carinate, the carinae on pereon segments 6 and 7 produced into teeth; gnathopod 1 (Fig. 2G) slender, chelate, article 2 with a small protuberance on anterior margin, article 3 elongate, 6 as long as 3-5 together; gnathopod 2 (Fig. 2H, I) very elongate and slender, simple, article 3 elongate, 7 tapering to an acute point which bears hooked setae; pereopods 1 and 2 powerful, article 4 slightly produced antero-distally; pereopods 3 and 4 with article 2 greatly lobed postero-distally so as to obscure most of articles 3 and 4; (pereopod 5 missing on both sides).

Pleon segments strongly carinate mid-dorsally, each with a pair of latero-dorsal humps; first pleonal epimeron postero-distally produced into a rounded lobe, the second acutely produced, a rounded lobe in centre of posterior margin; third pleonal epimeron postero-distally rounded, slightly produced; urosome

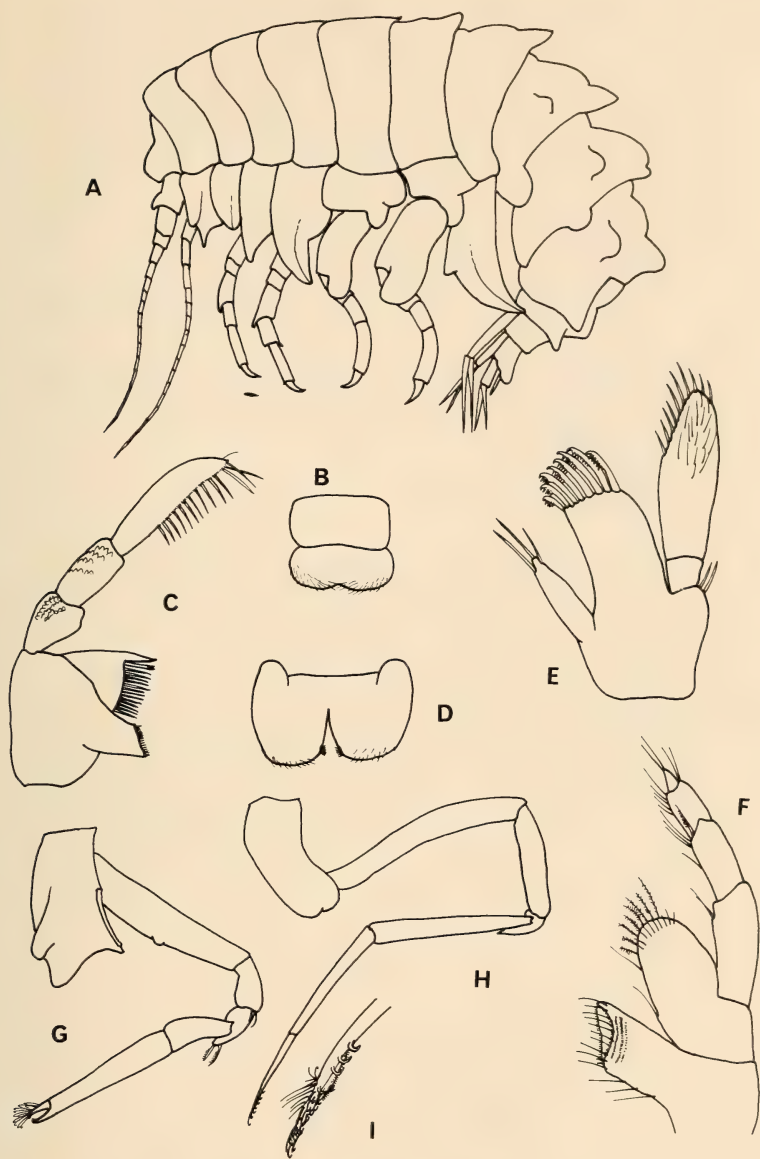


Fig. 2. *Dikwa acrania* n. gen., n. sp.
 Female, 3 mm: A—lateral aspect; B—upper lip; C—mandible; D—lower lip;
 E—maxilla 1; F—maxilliped; G—gnathopod 1; H—gnathopod 2; I—tip of
 article 7 of gnathopod 2 enlarged.

strongly deflexed beneath pleon, segment 1 longer than 2 plus 3 and bearing a medio-dorsal and a pair of latero-dorsal humps, segments 2 and 3 smooth; uropods elongate, unarmed, rami narrow-lanceolate, projecting equally; telson slightly longer than broad, apically emarginate.

The entire integument appears to be composed of small plates, in places bearing a resemblance to the scales of a fish.

Colour: Uniform white (as preserved in 70% alcohol).

Holotype: SAM A13213, female, 3 mm.

Type locality: SST 11W, 32°22'S/22°31'E, 20 June 1972, depth 200 m, substrate coarse khaki sand.

Remarks: This unusual species can easily be recognized by the markedly reduced head. In life the antennae are flexed beneath the pereon so that the animal appears to have had its head broken off.

Material: 2 ♀♀ from the type locality.

Iphimedia capicola K. H. Barnard, 1932

Iphimedia capicola K. H. Barnard, 1932; 118, fig. 66.

Records: SCD 160B(1), SCD 181T (1), SCD 216N(1); SST 16M(4).

Diagnosis: Rostrum acute, downturned; article 1 of antenna 1 terminating in one dorsal and two ventral teeth, flagellum 12-articulate; pereon segments 1 and 7 much longer than other segments; pereon segment 7 and pleon segments 1–3 each with a pair of procumbent dorsal teeth; pleon segments dorsally keeled; postero-distal corner of third pleonal epimeron produced into an upturned tooth, a second upturned tooth on posterior margin of the epimeron; telson apically truncate, a pair of small denticles on each margin near the apex.

Distribution: Endemic to south and west coasts of South Africa.

Family Ampeliscidae

Ampelisca acris n. sp.

Fig. 3

Ampelisca excavata: K. H. Barnard, 1955: 82, fig. 40A.

(non) *Ampelisca excavata* K. H. Barnard, 1925: 336, pl. 34, figs 5–7. Gray & J. L. Barnard, 1970: 67–83, figs 1–5, pl. 1.

Description of female (11 mm): Head as long as two pereon segments (Fig. 3A), antero-ventral margin oblique; two pairs of eyes with corneal lenses, the lower pair just behind lateral angles of head, a small pigment spot behind upper eye; antenna 1 extending well beyond peduncle of antenna 2, flagellum 19-articulate;

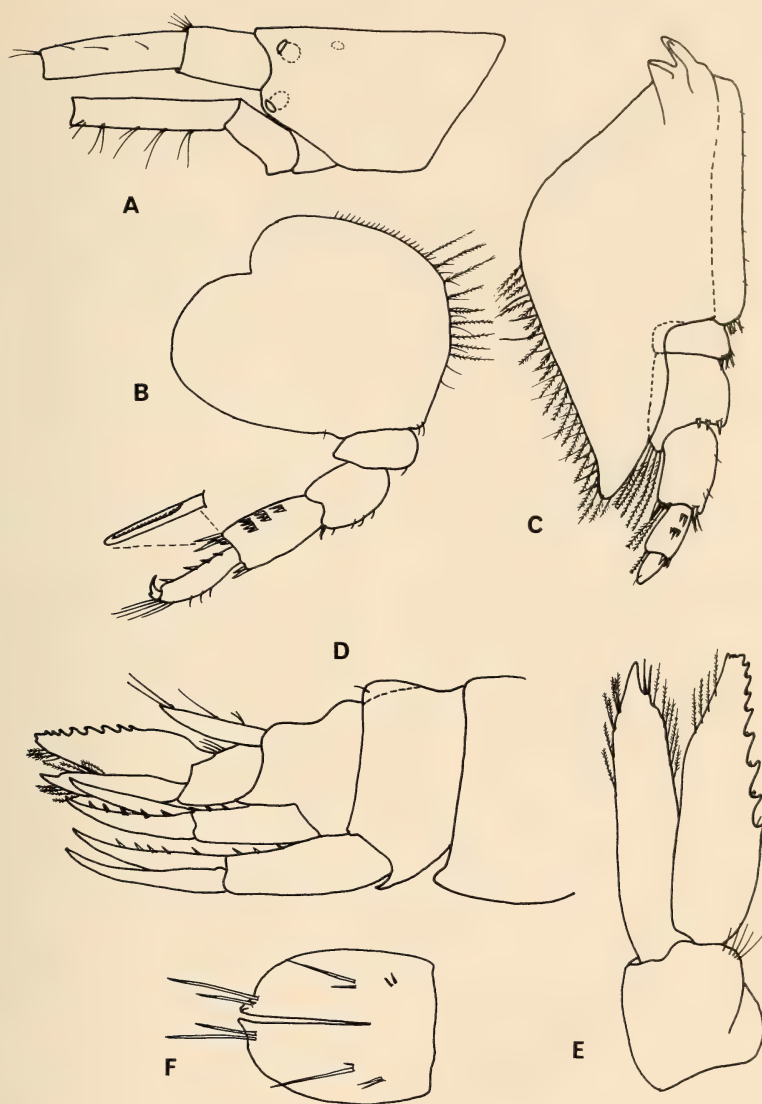


Fig. 3. *Ampelisca acris* n. sp.
Female, 11 mm: A—head; B—pereopod 3; C—pereopod 5; D—lateral view of
urosome; E—uropod 3; F—telson.

antenna 2 about half length of body, flagellum 20-articulate; mandibular palp borne on a large process, article 1 half as long as 2, article 3 60% length of 2, spine row of nine spines; outer plate of maxilla 1 with 11 spines, palp terminating in four cusp teeth, four blunt spines and about 10 setae; inner plate of maxilliped extending to tip of article 1 of palp, armed with two blade-like spines, outer plate bearing 10 spines ranging from short and blade-like proximally to long and evenly tapering distally.

Gnathopod 1 moderately setose, article 6 ovate, half as wide as long; dactyl less than half length of article 6 and bearing three accessory setae; gnathopod 2 more slender than 1, article 6 half length of 5, dactyl less than half article 6 and bearing six accessory setae; pereopod 1 not heavily setose, article 4 with antero-distal angle slightly produced, article 7 equal to 5 plus 6; coxae 1-3 each with a postero-distal tooth; article 2 of pereopod 3 (Fig. 3B) as wide as long, article 5 bearing four rows of spines posteriorly, the spines in the terminal row serrate, article 6 with a row of four spines along its hind margin, dactyl bifurcate; pereopod 4 very like 3 but with a shorter article 6 which bears spines on its anterior as well as posterior margin; pereopod 5 (Fig. 3C) with an unusual article 2 projecting to an acute point in line with the distal end of article 5, posterior margin slightly concave distally, anterior edge of the lobe partially obscuring articles 3 and 4, article 4 almost twice length of 3, its postero-distal corner slightly produced and bearing four plumose setae, article 5 equal to 4 and bearing an antero-distal spine and a postero-distal group of three spines and two plumose setae, article 6 slightly shorter than 5, two groups of spines on outer margin, article 7 short and wide.

Third pleonal epimeron very slightly produced postero-distally; pleon segment 4 weakly crested dorsally (Fig. 3D); uropod 1 projecting to end of uropod 2, rami equal, subequal to peduncle, inner ramus dorsally spinose; rami of uropod 2 equal, the outer dorsally spined; uropod 3 (Fig. 3E) with equal rami, the outer slightly the more slender, apically acute and setose on both margins, inner ramus with its upper margin cut into eight strong cusps, a minute accessory tooth in each hollow, tip of ramus serrate, its lower-distal margin bearing four plumose setae; telson 70% cleft (Fig. 3F), each lobe bearing 2 long apical setae and with two pairs of smaller setae on the dorsal surface.

Holotype: SAM A13206, female, 11 mm.

Type locality: MB 50Q, 34°11'S/22°09'E, 17 January 1956, depth 10 m, substrate rocky.

Relationships: There has been considerable confusion in the past between this species and *Ampelisca excavata* K. H. Barnard, 1925. K. H. Barnard's description of *A. excavata* was based on a single specimen, and when larger specimens of an apparently similar form were collected he ascribed these to the same species, concluding that his original specimen must have been abnormal (K. H. Barnard 1955).

Subsequently it has been found that these two batches of material represent distinct species. K. H. Barnard's original *A. excavata* has been redescribed in great detail by Gray & J. L. Barnard (1970) while his 1955 material is hereby renamed *Ampelisca acris* n. sp.

As can be readily appreciated by comparing Figure 3 with the illustrations in Gray & J. L. Barnard (1970), the two forms are quite distinct. *A. excavata* is altogether a stouter species with a bifurcation at the tip of article 2 of pereopod 5, a reduced inner ramus of uropod 1 and heavily chitinized rami on uropods 2 and 3. As well as differing in the structural features mentioned above, the two species can be distinguished by their modes of life, *A. acris* being a free-living tube builder, whereas *A. excavata* appears to be restricted to cirripede burrows in the shells of large molluscs such as *Turbo sarmaticus* Linn. and *Haliotis midae* Linn.

Material: SCD 160G(2); LIZ 17E(4); MB 50Q(3), MB 54X(1), MB 66V(1).

Ampelisca anisuropa (Stebbing, 1908)

Byblis anisuropus Stebbing, 1908a: 72, pl. 10. K. H. Barnard, 1955: 82, fig. 40B.

Ampelisca anisuropa: Griffiths, 1974a: 220.

Records: SCD 104X(1), SCD 173X(1), SCD 188D(2), SCD 204K(3), SCD 211Z(1), SCD 232C(4), SCD 321Q(2), SCD 392U(2); SST 5J(1), SST 9F(1), SST 16E(2); 33°S/28°E/86 m (Stebbing 1908a).

Distribution: Endemic, Natal to west coast of South Africa.

Ampelisca anomala Sars, 1882

Ampelisca anomala: Sars, 1895: 178, pl. 62, fig. 2.

Records: SCD 24J(1), SCD 41L(4); LIZ 29Q; MB 57E(1), MB 50R(1).

Diagnosis: Head with post-antennal corner acute; two pairs of eyes with large corneal lenses, the lower pair directed laterally; antennae fairly long, antenna 1 half as long as body, 2 slightly shorter than body; none of coxae with distal teeth; article 2 of pereopod 5 distally rounded, 3 longer than 4, 4 not produced distally, 6 equal to 4 plus 5, 7 of moderate size; third pleonal epimeron quadrate postero-distally; pleon segment 4 with a distinct triangular dorsal carina; telson 80% cleft, a single spinule at apex of each lobe.

Distribution: Scandinavia, South Africa.

Ampelisca brevicornis (Costa, 1853)

Ampelisca brevicornis: Reid, 1951: 204–210, figs 9–15. Kaim Malka, 1969: 928–932, pls 1–6.

Records: SCD 24K(9), SCD 95C(1), SCD 103W(1), SCD 122E(1), SCD 148K(4), SCD 160F(1), SCD 198E(1), SCD 202E(1), SCD 219F(3), SCD 222H(15), SCD 225H(12), SCD 244B(155), SCD 248H(20), SCD 257M(5), SCD 276M(3),

SCD 278J(3), SCD 315V(102), SCD 329V(2), SCD 338L(5), SCD 343T(1), SCD 349R(1), SCD 353M(1), SCD 366T(1), SCD 368V(1), SCD 370K(6), SCD 379N(1), SCD 381P(1), SCD 391F(4); SST 29E(42), SST 32F(5), SST 34F(14), SST 40S(10), SST 41N(1), SST 45D(8), SST 62M(2), SST 65B(4), SST 68N(2); 34°S/22°E/?m (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Ampelisca chiltoni Stebbing, 1888

Ampelisca chiltoni: J. L. Barnard, 1961: 61, fig. 31.

Records: SCD 160E(1), SCD 232A(2), SCD 262G(1), SCD 356N(22), SCD 359A(1), SCD 392X(15); SST 1D(10), SST 5B(24), SST 9C(16), SST 16F(8), SST 47H(1); LIZ 32W(11); 32°S/28°E/86 m (Stebbing 1918).

Distribution: Australia, New Zealand, South Africa.

Ampelisca diadema (Costa, 1853)

Ampelisca diadema: Chevreux & Fage, 1925: 82, fig. 74.

Records: LIZ 32X(11).

Distribution: Europe, southern Africa.

Ampelisca fusca Stebbing, 1888

Ampelisca fusca Stebbing, 1888: 1052, pl. 105.

Records: SCD 181J(26), SCD 204L(20), SCD 235X(3), SCD 253G(1), SCD 269S(1), SCD 273E(1), SCD 300P(34), SCD 302T(1), SCD 321R(1); SST 19A(230), SST 24A(260), SST 34P(7).

Distribution: Endemic, Moçambique to South West Africa.

Ampelisca natalensis K. H. Barnard, 1916

Ampelisca natalensis K. H. Barnard, 1916: 137, pl. 26, fig. 7.

Records: LIZ 19P(1), LIZ 29O(1).

Distribution: Endemic, Natal to Port Elizabeth.

Ampelisca palmata K. H. Barnard, 1916

Ampelisca palmata K. H. Barnard, 1916: 136, pl. 28, figs 30–31.

Records: SCD 41M(6), SCD 93M(1), SCD 115F(2), SCD 141V(2), SCD 188C(10), SCD 192V(1250), SCD 193W(2), SCD 198F(3), SCD 204M(14), SCD 219G(7), SCD 232B(1), SCD 235W(17), SCD 248J(70), SCD 321P(1),

SCD 343R(47), SCD 356P(12), SCD 376L(7), SCD 381Q(1), SCD 383T(2), SCD 392Y(1); SST 56S(1); MB 10Q(1); ZZ 3U; 32°S/28°E/94 m (K. H. Barnard 1916).

Distribution: Senegal to Moçambique.

Ampelisca spinimana Chevreux, 1887

Ampelisca spinimana: Chevreux & Fage, 1925; 81, fig. 73.

Records: SST 45J(4); KNY 245H(1); BMR 23T(1).

Distribution: Europe, West and South Africa.

Byblis gaimardi (Kröyer, 1846)

Byblis gaimardi: Mills, 1971: 367–370, figs 6A, 7.

Records: SCD 300R(4), SCD 302X(1); 32°S/28°E/94 m (K. H. Barnard 1916).

Distribution: Arctic, North Atlantic, ? Pacific, South Africa.

Family **Amphilochidae**

Cyproidea ornata Haswell, 1880

Cyproidea ornata: J. L. Barnard, 1972a: 21, figs 4, 5.

Records: SCD 216D(13); J 11F; K 8P; E 223; L 504; Port Alfred, East London (K. H. Barnard 1940).

Distribution: Indo-Pacific, extending to South West Africa.

Gitanopsis mariae Griffiths, 1973

Gitanopsis mariae Griffiths, 1973: 275, fig. 4.

Records: SST 11X(5), SST 24Q(1).

Distribution: Endemic, Moçambique to Still Bay.

Gitanopsis pusilla K. H. Barnard, 1916

Gitanopsis pusilla K. H. Barnard, 1916: 144.

Records: SCD 55K(1), SCD 74J(2), SCD 173Y(28), SCD 198Y(3), SCD 392Z(1); SST 32M(1), SST 37W(4); HAV 3C(1); SS 55C; Still Bay (K. H. Barnard 1940).

Distribution: Southern Atlantic, southern Indian Ocean.

Hoplopleon medusarum K. H. Barnard, 1932

Hoplopleon medusarum K. H. Barnard, 1932: 105, fig. 54.

Records: SCD 338K(1); SST 16B(3).

Distribution: Endemic, south coast of South Africa to South West Africa.

Family **Ampithoidae***Ampithoe africana* K. H. Barnard, 1925

Ampithoe africana K. H. Barnard, 1925: 361.

Records: KNY 166F; Y 12G; East London (K. H. Barnard 1925).

Distribution: Endemic, Natal to Knysna.

Ampithoe falsa K. H. Barnard, 1932

Ampithoe brevipes: K. H. Barnard, 1916: 255, pl. 28, fig. 34.

Ampithoe falsa: Ruffo, 1969: 57, figs 18–20.

Records: LLL 6L; SS 55H; Still Bay (K. H. Barnard 1940).

Distribution: Indian Ocean.

Ampithoe ramondi (Audouin, 1826)

Ampithoe intermedia: Stebbing, 1910a: 462.

Ampithoe vaillanti: K. H. Barnard, 1916: 253.

Ampithoe ramondi: J. L. Barnard, 1970b: 50, figs 18, 19.

Records: SCD 20U(1); MB 10S(1), MB 40L(3), MB 58Q(1), MB 59F(1); LIZ 40F; L 493B; 33°S/26°E/18–29 m (Stebbing 1910a).

Distribution: Circumtropical.

Cymadusa filosa Savigny, 1818

Grubia australis K. H. Barnard, 1916: 258.

Cymadusa australis: K. H. Barnard, 1940: 480.

Cymadusa filosa: J. L. Barnard, 1955: 29, fig. 15.

Records: KNY 6L, KNY 11H, KNY 30A, KNY 122A, KNY 128A, KNY 139C(9), KNY 162A, KNY 179D(10), KNY 245G(4), KNY 283K(3); Knysna Lagoon (K. H. Barnard 1940).

Distribution: Circumtropical.

Macropisthopus stebbingi K. H. Barnard, 1916

Macropisthopus stebbingi K. H. Barnard, 1916: 260, pl. 28, figs 15–17.

Records: ZZ3R; SS 55K; Port Elizabeth (K. H. Barnard 1916); Still Bay (K. H. Barnard 1940).

Diagnosis: This species is the only representative of the genus, which is diagnosed as follows: antenna 1 without accessory flagellum; mandible with palp; both

gnathopods very feebly chelate; article 6 of pereopods 3–5 scarcely widened; pereopod 5 greatly enlarged, flattened; outer ramus of uropod 3 bearing two large hooks.

Distribution: South coast of South Africa.

Family Cheluridae

Chelura terebrans Philippi, 1839

Chelura terebrans: Chevreux & Fage, 1925: 371, figs 379, 380.

Records: Port Elizabeth harbour (Stebbing 1910a).

Diagnosis: Head with large frontal process; pleon segment 1 with large medio-dorsal posteriorly directed process; urosome segments fused; uropods differing radically from one another in size and form; uropod 2 with short subequal rami, peduncle with large marginally setose winglike lobe; uropod 3 enormous, outer ramus very large, inner ramus small.

Distribution: Cosmopolitan.

Family Colomastigidae

Colomastix keiskama n. sp.

Fig. 4

Description of male (4 mm): Head with anterior keel projecting between the antennae, eyes of moderate size, brown (in alcohol), lateral cephalic lobes evenly rounded; antenna 1 lacking spines, articles 1–3 each with a pair of ventral keels distally produced into small teeth, flagellum of a single terminally setose article; antenna 2 smooth, slightly shorter than 1; mandible (Fig. 4B) cut into five strong teeth, the first terminally bifurcate; maxilliped (Fig. 4C) with inner plates coalesced, outer plates each bearing a single terminal seta.

Coxae 1–6 smoothly rounded, oval, coxa 6 produced posteriorly into a semi-acute point (Fig. 4A); articles 5 and 6 of gnathopod 1 subequal, article 6 terminating acutely in about five setae; article 2 of gnathopod 2 faintly crenulate anteriorly, article 5 unusually large, bearing a wide setose posterior lobe, article 6 not more than 1.5 times the size of 5, as wide as long, palm about equal to hind margin, defined by three small cusps and bearing two subequal teeth near finger hinge, dactyl equal to palm; pereopod 3 smaller than 4 or 5, article 2 oval.

Pleonal epimeron 1–3 broadly rounded; uropod 1 with inner ramus terminating in a strong blade-like spine about 50 per cent length of body of ramus; uropods 2 and 3 projecting about equally and well beyond the tip of uropod 1, inner ramus of each marginally the longer and with its upper margin finely serrate; telson smoothly rounded (Fig. 4D).

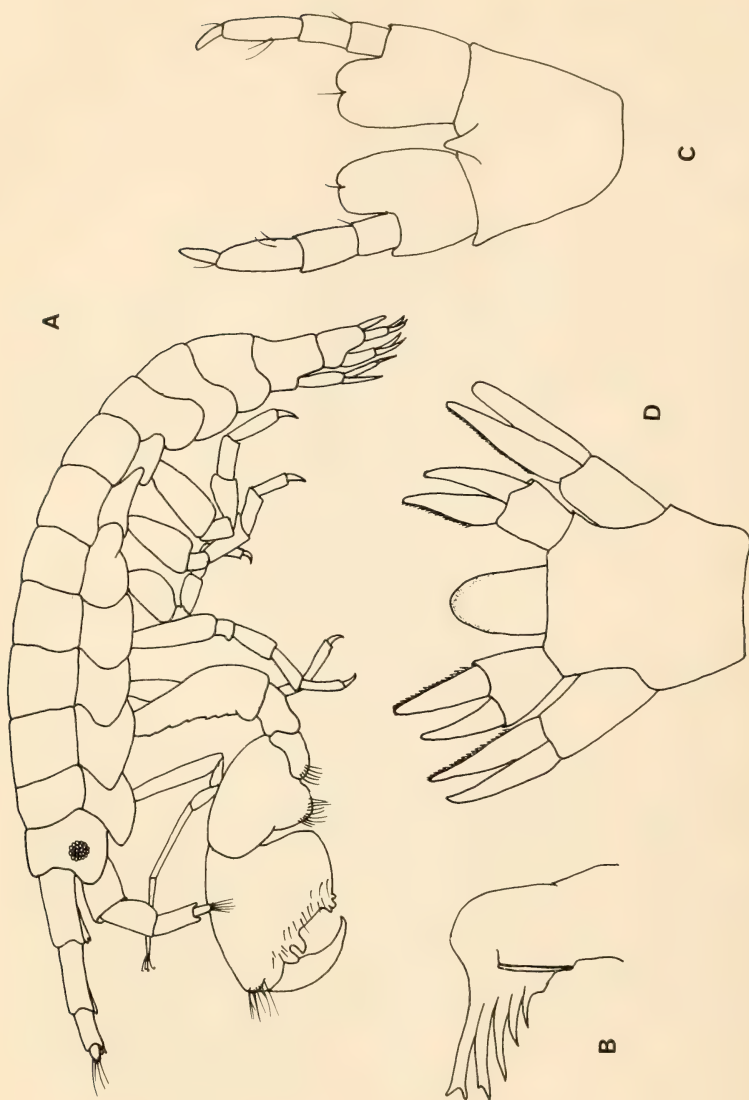


Fig. 4. *Colomastix keiskama* n. sp.
Male, 4 mm: A—lateral aspect; B—maxilliped; C—mandible; D—fused urosomites 2 and 3 and telson in dorsal view.

Holotype: SAM A13208, male, 4 mm.

Type locality: SCD 179J, 33°59'S/25°41'E, 24 November 1960, depth 4–11 m, substrate rocky.

Relationships: The second gnathopod and first uropod are of most unusual structure and immediately distinguish this species from its relatives. Other species with equal rami of uropod 3 and an unsculptured telson include *C. pusilla*

Grube and *C. simplicauda* Nicholls but their second gnathopods are quite different from those of *C. keiskama* n. sp.

Material: SCD 179J, a single male.

Colomastix pusilla Grube, 1864

Colomastix pusilla: J. L. Barnard, 1971: 55, fig. 24.

Records: SCD 159U(20).

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Corophiidae**

(Revised J. L. Barnard 1972b)

Aora typica Kröyer, 1845

Aora typica: J. L. Barnard, 1969b; 148, fig. 63.

Records: SCD 62C(1), SCD 118N(1), SCD 135D(1), SCD 148J(2), SCD 159Y(3), SCD 181V(4), SCD 198H(2), SCD 208G(1), SCD 225J(4), SCD 232D(1), SCD 244K(2), SCD 257H(5), SCD 276Q(2), SCD 287C(2), SCD 310H(1), SCD 321T(1), SCD 326K(1), SCD 338H(3), SCD 339R(2), SCD 353P(3), SCD 368V(1), SCD 379M(1), SCD 381S(6), SCD 392Z(2); SST 16P(1), SST 32B(1), SST 34J(1), SST 37U(5); LIZ 29R(2); T 13J; SS 55G.

Distribution: Cosmopolitan.

Camacho bathyplous Stebbing, 1888

Camacho bathyplous: J. L. Barnard, 1961: 115, figs 81, 82.

Records: 33°S/28°E/86 m (Stebbing 1908a).

Diagnosis: This genus is monotypic, the diagnosis being: antenna 1 elongate, greatly exceeding antenna 2, article 1 much longer than 3, accessory flagellum multi-articulate; mandibular palp 3-articulate; coxae short, serially discontinuous; gnathopods subchelate, uropods biramous, the third with inner ramus 30% length of outer.

Distribution: Indo-Pacific.

Cerapus tubularis Say, 1818

Cerapus abditus: K. H. Barnard, 1916; 271.

Cerapus tubularis: J. L. Barnard, 1962: 61, figs 27, 28.

Records: SCD 41K(3), SCD 60H(4), SCD 81B(1), SCD 159Z(1), SCD 244A(25), SCD 257J(3), SCD 262M(1), SCD 267L(2), SCD 312P(5), SCD 338E(1), SCD 342F(4), SCD 343V(4), SCD 353C(20); SST 32E(1); LIZ 13U(1).

Distribution: Cosmopolitan in warm and temperate seas.

Cheiriphotis megacheles (Giles, 1885)

Cheiriphotis megacheles: J. L. Barnard, 1962: 17, fig. 4.

Records: SCD 20M(10), SCD 20L(2), SCD 34D(1), SCD 34G(1), SCD 60J(20), SCD 62A(C), SCD 64B(C), SCD 81D(2), SCD 95J(18), SCD 124U(4), SCD 124V(1), SCD 189R(38), SCD 192Y(1), SCD 257G(101), SCD 278K(2), SCD 282S(10), SCD 283F(18), SCD 285S(4), SCD 312Q(7), SCD 329W(2), SCD 332S(15), SCD 338G(181), SCD 339Q(9), SCD 353F(14), SCD 379J(10), SCD 383V(1), SCD 391K(1); SST 45F(2); LIZ 3Z(12), LIZ 31S(1); MB 4U(4), MB 5H(4), MB 28G(8), MB 33N(1), MB 45E(1), MB 46F(1), MB 59H(1), MB 71K(2), MB 73M(7), MB 75K(4), MB 77Q(3), MB 80D(6).

Distribution: Indo-Pacific.

Chevalia aviculae Walker, 1904

Chevalia aviculae: J. L. Barnard, 1971: 88, fig. 42.

Records: SCD 62D(1), SCD 99N(4), SCD 181U(2), SCD 244J(5), SCD 302V(1), SCD 304R(18), SCD 308J(1), SCD 311J(2), SCD 366X(1); SST 16A(9), SST 19H(1), SST 24L(6), SST 47E(1); 34°S/23°E/230 m (K. H. Barnard 1916).

Distribution: Cosmopolitan in tropical and temperate seas.

Concholestes armatus n. sp.

Figs 5, 6

Description of male (6 mm): Ocular lobes of head strongly produced obliquely downwards, eyes small, black; antennae very large (Fig. 5A), 1 slightly shorter than body, articles 1 and 2 subequal, longer than 3, flagellum 12-articulate; antenna-2 longer than body, very sturdy, used to drag the animal and its *Dentalium* shell abode across the sea floor, flagellum of one long and one short article; mandible (Fig. 6A) bearing large molar composed of rows of sharp tubercles, palp uni-articulate, bearing long plumose setae; maxilla 1 (Fig. 6B) with bi-articulate palp, article 2 terminating in six strong serrate spines, outer plate also ending in six strong serrate spines, inner plate smooth; plates of maxilla 2 subequal, the inner with an oblique row of 16 setae medially (Fig. 6C), both plates terminally setose; maxilliped (Fig. 6D) with 4-articulate palp, inner plate with three terminal blade spines, outer plate with proximal spines blade-like, the more distal ones becoming longer and more slender.

Coxae 1 and 2 produced forwards, marginally setose; gnathopod 1 simple (Fig. 5B), article 5 longer than 6, dactyl extremely large, bearing seven strong spines along its posterior margin; gnathopod 2 (Fig. 5C) subchelate, article 2 broad, six very strong spines and one small one forming a comblike row along anterior margin, article 3 bearing two anterior spines, article 6 longer than 5,

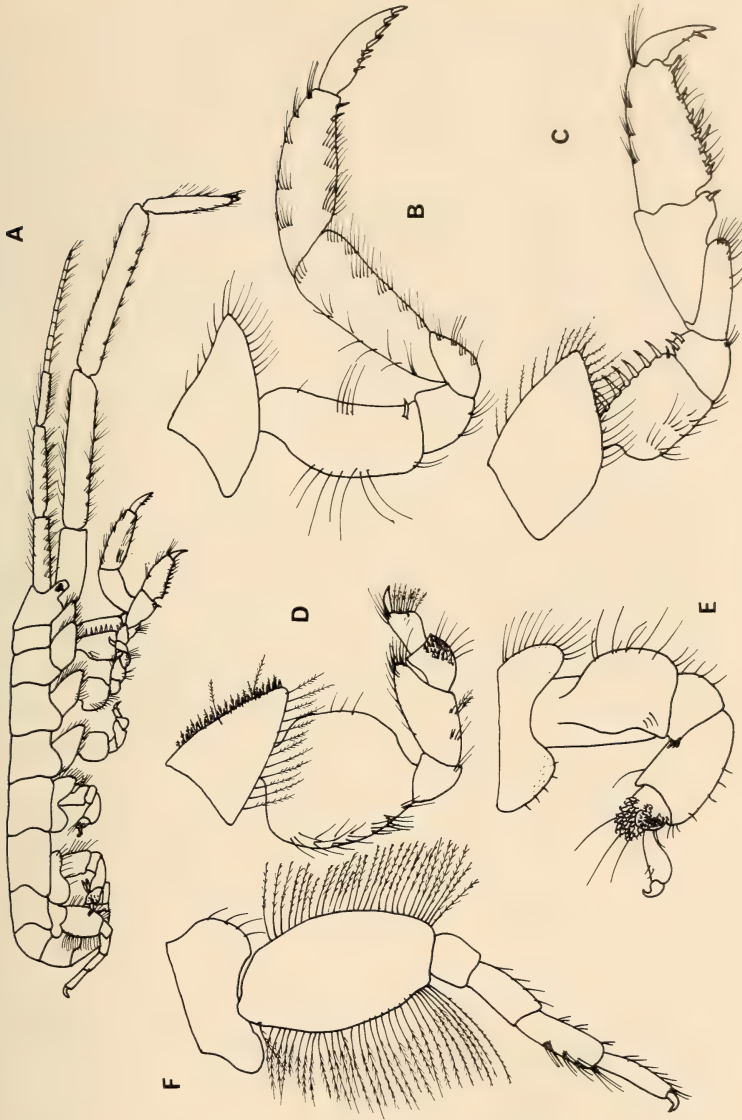


Fig. 5. *Concholestes armatus* n. sp.
Male, 6 mm: A — lateral aspect; B — gnathopod 1; C — gnathopod 2; D — pereiopod 1; E — pereiopod 3; F — pereiopod 5.

widest at its base, palm spinose, dactyl shorter than palm, bearing a distal spine; coxa 3 anteriorly lined by a row of short spines and setae, posterior margin lined by long plumose setae; article 2 of pereiopod 1 subcircular (Fig. 5D), article 5 posteriorly covered in short thick spines; coxa 4 triangular, not spinose; pereiopod 2 like 1; pereiopod 3 small, directed posteriorly (Fig. 5E), article 5 bilobed, outer lobe covered in minute spines, inner lobe bearing many large hooked spines; pereiopod 4 similar to 3 but somewhat larger; pereiopod 5 (Fig. 5F) elongate, article 2 strongly setose.

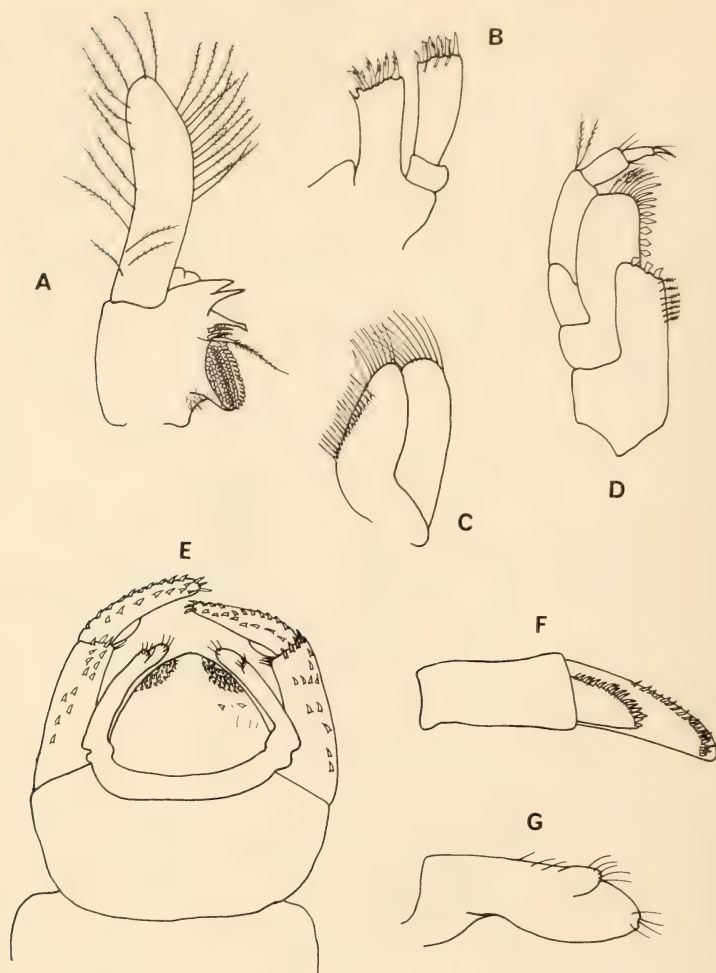


Fig. 6. *Concholestes armatus* n. sp.

Male, 6 mm: A—mandible; B—maxilla 1; C—maxilla 2; D—maxilliped; E—dorsal view of urosome; F—ventral view of uropod 1; G—uropod 2 as seen laterally.

Pleonal epimera rounded, setose; urosome (Fig. 6E) reduced, tucked between pereopods, only two segments present; segment 1 bearing a pair of large biramous uropods, both peduncle and rami heavily spinose (Fig. 6E, F), inner ramus 50% length of outer; second urosome segment less than half length of first, bearing a pair of laterally flattened uropods represented by a distally bilobed peduncle (Fig. 6E, G); telson very large, squamous, laterally strongly spinose.

Female: Ovigerous at 4 mm: the eggs are restrained by the pereopods which angle in ventrally to form a tunnel beneath the body, the brood lamellae are

reduced to narrow lobes. In one case newborn young were found to occupy the narrow end of a *Dentalium* shell in which a large female was living.

Holotype: SAM A13207, male, 6 mm (13 mm including antennae).

Type locality: SST 1B, 35°22'S/22°31'E, 20 June 1972, depth 200 m, substrate coarse khaki sand.

Relationships: This species closely resembles *C. dentali* Giles in its habits and in its unusually strong antennae and reduced third uropods. Unfortunately, however, Giles's description of the urosome of his species is unclear and he fails to describe its mandibular palp. The urosome is described as follows: '4th abdominal appendage biramous; 6th blunt, rounded, without rami, nearly hidden beneath the squamous telson . . . of the fifth abdominal appendage I have been unable to obtain a satisfactory view, it is small and its peduncle is very short, though of considerable width. The ramus appears to be single and rounded.'

Despite his mention of a third uropod Giles's figure of the urosome (also reproduced by J. L. Barnard, 1969b) shows only two urosome segments and two pairs of uropods. Assuming Giles's verbal description of this unexpected and difficult to observe urosome to be erroneous, I have not erected a new genus for my species, especially since the chances of two distantly related forms occupying an identical niche seem remote. Should re-examination of *C. dentali* reveal a third urosomite or a mandibular palp of more than 1 article, this would necessitate the erection of a new genus for *C. armatus*.

Material: SST 1B(4), SST 5A(1), SST 11N(7).

Corophium acherusicum Costa, 1857

Corophium acherusicum: J. L. Barnard, 1971: 59, figs 17, 26.

Records: LIZ 1K(2); MB 87N(1).

Distribution: Cosmopolitan in tropical and temperate seas.

Corophium triaenonyx Stebbing, 1904

Corophium triaenonyx Stebbing, 1904: 25, pl. 6A.

Records: SUN 5E(1); BMR 25G(2); HAV 3A(A), HAV 5B(2), HAV 7N(C), HAV 10D(C), HAV 18K(C); KNY 112B, KNY 139D, KNY 160A, KNY 166E, KNY 176D, KNY 181B, KNY 184B, KNY 191E; GBR 23D, GBR 37B(14), GBR 46A(2); STJ 15J(P), STJ 16G(C), STJ 26B(C), STJ 27L(2), STJ 31T(A), STJ 32B(C); Keurbooms River, Plettenberg Bay, Knysna (K. H. Barnard 1940).

Distribution: Atlantic, Mediterranean, Indian Ocean.

Erichthonius brasiliensis (Dana, 1853)

Erichthonius brasiliensis: J. L. Barnard, 1971: 61, fig. 17E.

Records: LIZ 40E(10); MB 40V(1), MB 50W(C), MB 87B(4); KNY 139E; L 458B; 32°S/26°E/18–29 m (Stebbing 1910a).

Distribution: Cosmopolitan in tropical and temperate seas.

Gammaropsis afra Stebbing, 1888

Eurystheus afer: Stebbing, 1910a: 461.

Gammaropsis afra: J. L. Barnard, 1970b: 170, fig. 108.

Records: 33°S/28°E/86 m, 33°S/26°E/18–29 m (Stebbing 1908a).

Distribution: Circumtropical.

Gammaropsis atlantica Stebbing, 1888

Eurystheus atlanticus: Stebbing, 1910a: 461.

Gammaropsis atlantica: J. L. Barnard, 1971: 91, figs 43–45.

Records: SCD 10S(4), SCD 34C(3), SCD 55D(1), SCD 81A(1), SCD 93P(1), SCD 95A(50), SCD 102D(3), SCD 103T(1), SCD 128Q(3), SCD 172V(1), SCD 181X(1), SCD 185J(1), SCD 204R(1), SCD 208K(5), SCD 222L(1), SCD 269R(2), SCD 280K(1), SCD 300Q(5), SCD 302P(26), SCD 304Q(1), SCD 319X(4), SCD 321N(3), SCD 324G(3), SCD 328G(1), SCD 345S(2), SCD 352A(2), SCD 353A(24), SCD 392R(13); SST 5G(4), SST 16D(4), SST 24C(1); LIZ 37L(2), LIZ 40B(2); MB 50X(1), MB 61U(C), MB 66P(1), MB 87D(5), MB 86C(1); 33°S/28°E/86 m, 33°S/26°E/18–29 m (Stebbing 1908a).

Distribution: Circumtropical.

Gammaropsis holmesi (Stebbing, 1908)

Eurystheus holmesi Stebbing, 1908a: 85, pl. 14A.

Eurystheus semidentatus K. H. Barnard, 1916: 250, pl. 28, figs 13, 14.

Records: SCD 62E(2), SCD 135K(1); LIZ 40H(2); 33°S/26°E/18–29 m (Stebbing 1908a).

Distribution: Endemic, Natal to Saldanha Bay.

Grandidierella bonnieroides Stephensen, 1948

Grandidierella bonnieri: Ledoyer, 1967: 137, fig. 28A. Griffiths, 1973: 283; 1974b: 228.

(non) *Grandidierella bonnieri* Stebbing, 1908b: 120, pl. 16.

Grandidierella bonnieroides: Myers, 1970: 141, figs 1, 2.

Records: STJ 6A(A).

Distribution: Indian Ocean, Caribbean.

Remarks: Myers (1970) re-examined Stebbing's type material of *G. bonnieri* and found it to have only a single distal tooth on article 5 of gnathopod 1, as compared with the three distal teeth present in the material of Ledoyer and

Griffiths. These records are thus transferred to *G. bonnieroides* Stephensen. Myers further points out that different populations of *G. bonnieroides* from differing locations show variation in sternal armature, and that this factor is thus not of taxonomic significance.

Grandidierella chelata K. H. Barnard, 1951

Grandidierella chelata K. H. Barnard, 1951: 708, fig. 7.

Records: HAV 7H(A), HAV 17A(A); STJ 14A(A), STJ 15G(A), STJ 16H(P), STJ 27J(P).

Distribution: Endemic, Port St. Johns to South West Africa.

Grandidierella lignorum K. H. Barnard, 1935

Grandidierella lignorum K. H. Barnard, 1935: 300, fig. 14.

Records: BMR 23S(4), BMR 25J(1), BMR 26U(1); HAV 3B(C), HAV 9A(5), HAV 13K(A); KNY 101A, KNY 184A; GBR 46C(2); BRE 51M(3), BRE 52M(7), BRE 71M(C), BRE 77H(3), BRE 81A(C); STJ 8A, STJ 14B(P), STJ 15H(P), STJ 24K(P), STJ 27K(P); Keurbooms River, Plettenberg Bay (K. H. Barnard 1940).

Distribution: Estuaries around the Indian Ocean.

Lembos hypacanthus K. H. Barnard, 1916

Lembos hypacanthus K. H. Barnard, 1916: 237, pl. 28, figs 5, 6.

Lembos hirsutipes (non Stebbing 1895): K. H. Barnard, 1951: 706.

Records: KNY 13G, KNY 139B, KNY 166G, KNY 171F.

Distribution: Endemic, Natal to South West Africa.

Neomicrodeutopus nyala n. sp.

Fig. 7

Description of male (4 mm): Head anteriorly truncate, eyes circular with the centre black; mandible with 3-articulate palp, articles 1 and 3 subequal, shorter than 2, molar large, lacinia mobilis present (Fig. 7E), spine row of three spines; inner plates of maxilliped (Fig. 7F) with three apical blade-spines, outer plate with seven blade-spines along inner margin, the spines becoming progressively longer distally, palp 4-articulate, the terminal article bearing three strong setae; (antennae missing).

Coxae short, not touching serially; gnathopod 1 (Fig. 7B) powerful, article 5 postero-distally produced into two teeth separated by a semicircular concavity, article 6 much narrower than 5, bearing a small bump on posterior margin,

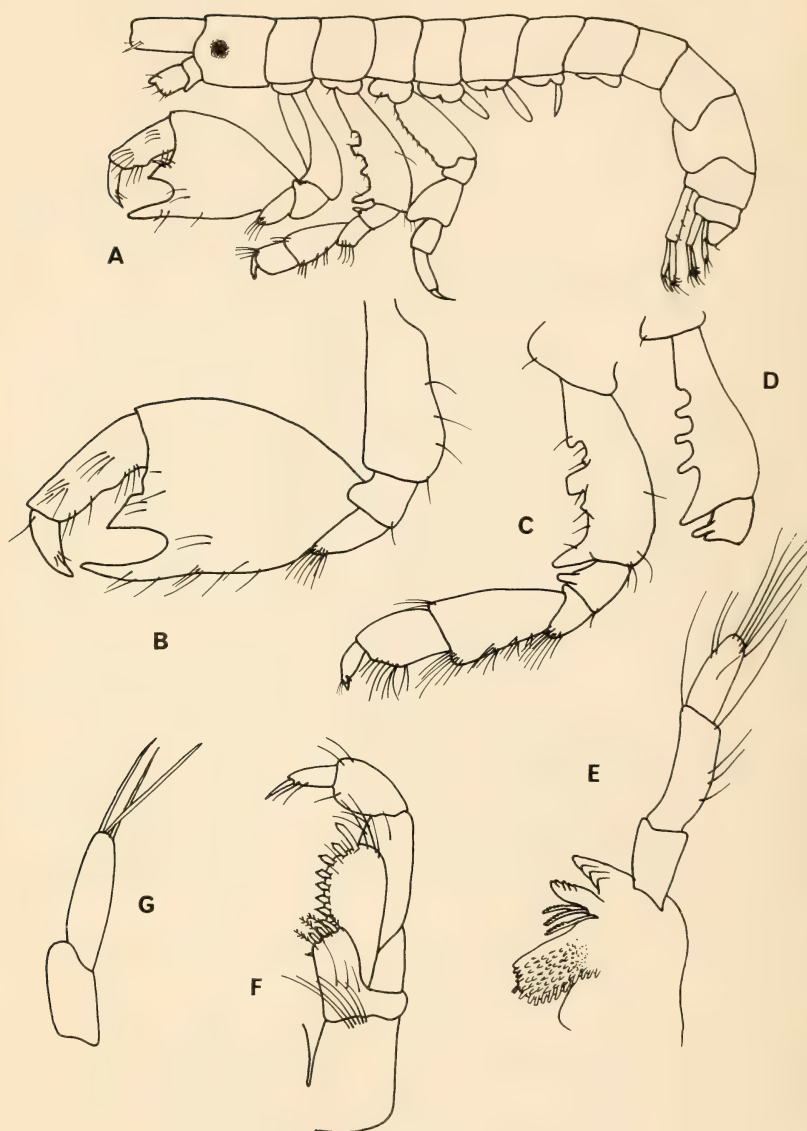


Fig. 7. *Neomicrodeutopus nyala* n. sp.
 Male, 4 mm: A—lateral aspect; B—gnathopod 1; C—gnathopod 2 left side;
 D—article 2 of gnathopod 2 right side; E—mandible; F—maxilliped;
 G—uropod 3.

7 shorter than 6; article 2 of gnathopod 2 (Fig. 7C) anteriorly produced into a number of projections (in this individual four fairly regular teeth on one side and three teeth on the other), the distal tooth the largest, article 3 anteriorly produced into an elongate lobe, article 5 longer than 6, palm oblique, not defined, dactyl terminating in a large spine and three setae; pereopod 1 stout, article 2 regularly crenulate anteriorly; (pereopods 2–5 missing).

Pleonal epimera smoothly rounded, somewhat lobed postero-distally; uropods 1 and 2 biramous, rami equal, terminally strongly spinose, uropod 1 with a terminal peduncular spine projecting between the rami; uropod 3 (Fig. 7G) uniramous, ramus twice length of peduncle, uni-articulate, three long setae at its apex; telson quadrangular, a dorsal tubercle and two or three short setae on each corner.

Holotype: SAM A13069, male, 4 mm.

Type locality: SST 34Q, 34°40'S/21°39'E, 21 June 1972, depth 80 m, substrate coarse shelly sand.

Relationships: The unusual armature of article 2 of gnathopod 2 immediately distinguishes this species from the other three members of the genus. In addition *N. nyala* n. sp. differs from *N. makaka* J. L. Barnard in the narrower article 6 of gnathopod 1 and the uni-articulate ramus of uropod 3, and from *N. cabindae* Schellenberg in the shape of article 5 of gnathopod 1. *N. elongata* (Chevreux) has more produced optic lobes and a much longer peduncle of uropod 3 than *N. nyala* n. sp.

Material: SST 34Q, 2 ♂♂.

Photis dolichommata Stebbing, 1910

Photis dolichommata Stebbing, 1910b: 609, pl. 55B.

Records: SCD 34E(6), SCD 41P(4), SCD 81C(2), SCD 100P(2), SCD 102H(5), SCD 103U(1), SCD 181S(8), SCD 204Q(5), SCD 208H(2), SCD 235Y(1), SCD 249U(1), SCD 295A(1), SCD 353B(260); SST 1A(3), SST 16T(1); 34°S/22°E/230 m (K. H. Barnard 1916).

Diagnosis: Ocular lobes very long, eyes oval, large; palm of gnathopod 1 male oblique, not excavate, dactyl finely serrate; article 2 of gnathopod 2 male not lobed antero-distally, palm slightly oblique, defined by a fairly strong tooth and with two small processes along its length; inner ramus of uropod 3 30% length of outer, outer ramus with a minute second article.

Distribution: Australia, South Africa.

Photis kapapa J. L. Barnard, 1970

Photis kapapa J. L. Barnard, 1970b: 192, figs 124, 125.

Records: SCD 282V(3), SCD 287E(4); SST 16U(1).

Distribution: Hawaii, east coast of southern Africa.

Photis longimanus Walker, 1904

Photis longimanus: K. H. Barnard, 1916: 244. Sivaprakasam, 1969: 567, fig. 8.

Records: SCD 192Z(40), SCD 204Z(1), SCD 244M(10), SCD 248K(3), SCD 257P(4), SCD 338Q(6), SCD 339T(4), SCD 368S(5).

Distribution: Indian Ocean, extending to South West Africa.

Photis uncinata K. H. Barnard, 1932

Photis longicaudata: K. H. Barnard, 1916: 243, pl. 28, fig. 26.

Photis uncinata K. H. Barnard, 1932: 223, fig. 138.

Records: SCD 24N(4), SCD 60L(2), SCD 83D(3), SCD 95D(30), SCD 99L(1), SCD 103V(1), SCD 122F(10), SCD 131Y(4), SCD 141T(1), SCD 146A(24), SCD 148M(1), SCD 151G(7), SCD 159X(3), SCD 181W(2), SCD 184E(2), SCD 188A(27), SCD 189A(135), SCD 216G(2), SCD 244P(5), SCD 302U(1), SCD 319Z(1), SCD 321U(2), SCD 343Z(2), SCD 345Z(6), SCD 353J(38), SCD 370S(3), SCD 379Q(1), SCD 392Z(8); SST 19B(6), SST 24D(3), SST 29F(4), SST 32G(1), SST 34K(3), SST 40U(2); 33°S/28°E/83 m, 34°S/23°E/80 m (K. H. Barnard 1916).

Distribution: Endemic to South Africa.

Siphonoecetes dellavallei Stebbing, 1893

Siphonoecetes dellavallei: Chevreux & Fage, 1925: 361, fig. 369.

Records: SCD 135J(3), SCD 198M(5), SCD 236C(3), SCD 285R(2), SCD 300W(1), SCD 338C(450), SCD 339V(7), SCD 368Q(30), SCD 383U(10), SCD 384S(9); SST 24M(1), SST 32D(1), SST 34N(1), SST 45A(33), SST 65G(1), SST 67Q(2), SST 73F(2); MB 5G(13), MB 34L(5).

Distribution: Mediterranean, southern Africa.

Siphonoecetes orientalis Walker, 1904

Siphonoecetes orientalis Walker, 1904: 294, pl. 7, fig. 49. K. H. Barnard, 1916: 270.

Records: SCD 95F(6), SCD 96W(1), SCD 120B(1), SCD 192Z(6), SCD 237H(1); 32°S/28°E/95 m, 34°S/26°E/116 m (K. H. Barnard 1916).

Distribution: Tropical Indo-Pacific.

Family **Dexaminidae***Atylus granulosus* (Walker, 1904)

Atylus granulosus: Ledoyer, 1967: 127, fig. 8.

Records: SCD 24Y(1); SST 37S(2), SST 47G(1), SST 60M(1); LIZ 31P(1).

Distribution: Indian Ocean.

Atylus guttatus (Costa, 1851)

Nototropis guttatus: Chevreux & Fage, 1925: 194, figs 201–203.

Records: SCD 285L(5), SCD 332V(34), SCD 339W(1), SCD 383N(141).

Distribution: Europe, West and South Africa.

Atylus homochir Haswell, 1885

Atylus homochir: Stebbing, 1888: 908–913, pl. 74.

Records: 33°S/26°E/18–29 m (Stebbing 1910a).

Diagnosis: Body dorsally carinate but carinae produced into teeth only on pereon segment 7 and pleon segments 1–3; pleon segment 4 with two dorsal teeth, the hind one the larger; composite pleon segment 5 and 6 with a posterior tooth; article 2 of pereopod 3 not at all produced postero-distally; pleonal epimera 1–3 each produced into a minute point postero-distally.

Distribution: Australia, South Africa.

Atylus swammerdami (Milne-Edwards, 1830)

Paratylus swammerdami: Sars, 1895: 463, pl. 163.

Atylus swammerdami: Chevreux & Fage, 1925: 195, fig. 204.

Records: MB 20V(1), MB 28F(4), MB 69S(1), MB 82B(17).

Distribution: Europe, West and South Africa.

Polycheria atolli Walker, 1905

Polycheria atolli: Ledoyer, 1972: 205, pl. 27.

Records: SCD 10R(5), SCD 55F(6), SCD 160A(11), SCD 172U(54), SCD 173T(8), SCD 181P(30), SCD 244H(51), SCD 262N(1), SCD 366P(1), SCD 379L(1), SCD 388D(1); SST 16L(1); LIZ 17F(3), LIZ 37N(1); MB 54V(C), MB 69Q(3), MB 77R(1), MB 86B(1), MB 87M(2); L 410; VV 2H; Still Bay (K. H. Barnard 1940).

Distribution: Southern oceans, extending to tropical Indian Ocean.

Family **Eusiridae***Eusirus minutus* Sars, 1893

Eusirus minutus: Sars, 1895: 419, pl. 149, fig. 2.

Records: SST 16Q(1).

Diagnosis: Pereon segment 7 and pleon segments 1 and 2 dorsally toothed; article 6 of gnathopods 1 and 2 attached to upper distal corner of article 5 ('eusirid'); third pleonal epimeron postero-distally rounded, lower posterior

margin finely serrate; article 6 of pereopods 3–5 less than twice as long as article 2; telson evenly tapering, less than 20% cleft, apices divergent.

Distribution: Norway, South Africa.

Eusiroides monoculoides (Haswell, 1880)

Eusiroides monoculoides: J. L. Barnard, 1964: 221, fig. 1.

Records: SCD 59C(2), SCD 181Z(3), SCD 253E(2), SCD 300N(18), SCD 312R(9), SCD 353Q(4), SCD 366Y(2); LIZ 29P(1); 32°S/28°E/170 m, 33°S/28°E/120 m, 34°S/25°E/137 m (K. H. Barnard 1916).

Distribution: Circumtropical.

Paramoera bidentata K. H. Barnard, 1932

Paramoera bidentata K. H. Barnard, 1932: 211, figs 118m, 129.

Records: Still Bay (K. H. Barnard 1940).

Distribution: Endemic, Still Bay to South West Africa.

Paramoera capensis (Dana, 1853)

Paramoera capensis: K. H. Barnard, 1916: 183–186.

Paramoera schizurus Stebbing, 1918: 66, pl. 10.

Records: SCD 24Q(14), SCD 110U(1), SCD 285N(5), SCD 332U(22), SCD 338Q(3), SCD 339U(2), SCD 381V(1), SCD 391P(5); SST 16G(10), SST 47F(2), SST 65D(2), SST 73J(1); LIZ 13Q(1), LIZ 29M(7), LIZ 32Y(1); MB 21D(1), MB 28D(C), MB 32J(2), MB 33M(2), MB 38H(C), MB 57B(17), MB 59G(2), MB 66Q(1), MB 70R(7), MB 71J(2), MB 73K(4), MB 82A(2), MB 87A(5); KNY 13F, KNY 57B, KNY 139A, KNY 166C, KNY 171B(C), KNY 179B(1); GBR 24H(7); BRE 135B(5); J 11J, Q 5J; LIZ 11Z; X 11B; K80; Y 12F; E 235; ZZ 3M; T 3F; RR 4H; KN 2G; KKN 43G; SS 4L, SS 55D; East London, Port Elizabeth (K. H. Barnard 1916); Still Bay (K. H. Barnard 1940).

Distribution: Atlantic and Indo-Pacific.

Family Gammaridae

Ceradocus rubromaculatus (Stimpson, 1855)

Ceradocus rubromaculatus: J. L. Barnard, 1972a: 220, fig. 129.

Records: SCD 55G(2), SCD 93L(3), SCD 110V(1), SCD 159S(2), SCD 181M(3), SCD 262H(6), SCD 300M(8), SCD 353G(5), SCD 366N(4), SCD 388C(1); SST 47B(8), SST 52P(1); LIZ 37K(1); MB 10R(2), MB 13N(1), MB 23G(2), MB 40K(2), MB 50T(2), MB 54T(10), MB 66M(12), MB 77S(1), MB 84U(1);

KNY 171A(1); QQ 4X; L 316; X 22E; E 229; ZZ 3T; T 3U; KN 43F; S 540; 33°S/25°E/45 m (Stebbing 1908a).

Distribution: Indo-Pacific.

Elasmopoides chevreuxi Stebbing, 1908

Elasmopoides chevreuxi Stebbing, 1908a: 82, pl. 39.

Records: 33°S/28°E/86 m (Stebbing 1908a).

Diagnosis: Accessory flagellum exceeding 20 articles; eyes extending almost whole height of head; article 3 of mandibular palp as long as 2, article 1 simple; inner plates of maxillae strongly setose medially; gnathopods subchelate; article 2 of pereopods 3–5 strongly dentate posteriorly; uropod 3 not exceeding uropod 1, rami broad, equal, the outer uni-articulate; lobes of telson basally separate.

Distribution: The above record is the only one of this species to date.

Elasmopus japonicus Stephensen, 1932

Elasmopus spinimanus (non Walker, 1905): K. H. Barnard, 1925: 358.

Elasmopus japonicus: Sivaprakasam, 1968: 278, figs 3–5.

Records: Y 12K; E 230; Port Elizabeth (K. H. Barnard 1940).

Distribution: Indo-Pacific, extending to South West Africa.

Elasmopus pecteniscrus Bate, 1862

Elasmopus pecteniscrus: J. L. Barnard, 1970a: 125, figs 73, 74.

Records: J 11H; QQ 4Z; L 47S; X 22A; SS 55E; Still Bay, East London (K. H. Barnard 1940).

Distribution: Cosmopolitan in tropical and temperate seas.

Eriopisa chilensis (Chilton, 1921)

Niphargus chilensis Chilton, 1921: 531, fig. 4.

Records: KNY 42A, KNY 81A.

Distribution: India, east coast of South Africa.

Eriopisa epistomata Griffiths, 1974

Eriopisa epistomata Griffiths, 1974a: 186, fig. 4.

Records: SCD 276 P(2); SST 40V(2), SST 41M(7).

Distribution: Endemic, south coast of South Africa to South West Africa.

Eriopisella capensis (K. H. Barnard, 1916)

Eriopisa capensis K. H. Barnard, 1916: 187, pl. 27, figs 16–19.

Records: SCD 222M(6), SCD 228B(19), SCD 232J(10), SCD 356S(2).

Diagnosis: Antero-lateral angles of head rounded, eyes absent; mandibular palp slender, article 3 shorter than 2; article 5 of gnathopod 1 not distally widened, 6 oval, palm oblique, three times as long as hind margin; gnathopod 2 with article 5 triangular, wider than 6; pleonal epimera postero-distally rounded; inner ramus of uropod 3 25% length of elongate outer ramus; telson cleft to base, lobes dehiscent, each bearing 3–4 unequal spines.

Distribution: Endemic to south and west coasts of South Africa.

Maera boeckii (Haswell, 1879)

Elasmopus boeckii: K. H. Barnard, 1916: 199, pl. 27, figs 13, 14.

Maera boeckii: K. H. Barnard, 1940: 460.

Records: S 54J; Port Elizabeth (K. H. Barnard 1916); Still Bay (K. H. Barnard 1940).

Diagnosis: Coxa 1 moderately produced forwards; palm of gnathopod 2 slightly oblique, bearing four strong teeth, that closest to the finger hinge having one or two accessory cusps, dactyl slender, closing within the defining tooth; posterior margin of third pleonal epimeron entire; uropod 3 not exceeding uropod 1; telson 60% cleft, lobes dehiscent, two setae arising from excavate tip of each lobe.

Distribution: Australia, South Africa.

Maera hamigera Haswell, 1880

Maera hamigera: K. H. Barnard, 1916: 196, pl. 27, fig. 11. J. L. Barnard, 1965: 507, fig. 16.

Records: SCD 262J(1), SCD 310G(20), SCD 343Z(1), SCD 373P(3), SCD 374K(5); 33°S/27°E/120 m (K. H. Barnard 1916).

Distribution: Indo-Pacific.

Maera inaequipes (Costa, 1851)

Maera inaequipes: J. L. Barnard, 1959a: 25, pl. 5.

Records: SCD 10E(12), SCD 10T(3), SCD 24L(1), SCD 41N(10), SCD 55E(10), SCD 102E(7), SCD 118P(1), SCD 181N(35), SCD 253D(1), SCD 300S(10), SCD 302Q(1), SCD 353N(3), SCD 370R(1); SST 16J(2), SST 24E(1); MB 54Z(6), MB 86A(2); 32°S/28°E/141 m, 33°S/28°E/91 m (K. H. Barnard 1916).

Distribution: Cosmopolitan in tropical and temperate seas.

Maera mastersi (Haswell, 1880)

Maera mastersi: Sivaprakasam, 1968: 36, fig. 1A–G. J. L. Barnard, 1972a: 226, fig. 132.

Records: SCD 34F(1), SCD 95G(1), SCD 159R(140), SCD 198Z(2), SCD 227P(1), SCD 269T(2), SCD 273H(2), SCD 321W(6), SCD 326L(2), SCD 366U(7); SST 16N(8), SST 19G(33).

Diagnosis: Coxa moderately produced forwards; gnathopod 2 much larger than 1, palm defined by a small projection, proximal portion of palm smoothly concave, covered by a dense fur of very short setae, distal third of palm produced into a small hump bearing two or three short spines; third pleonal epimeron bearing three posterior serrations; uropod 3 greatly exceeding 1 and 2; telson cleft nearly to base, a small notch on inner margin of each apex bearing a single seta.

Distribution: Indo-Pacific.

Remarks: The above specimens bear a close resemblance to those figured by Sivaprakasam (1968), although his figures fail to show any 'fur' of setae on the palm of gnathopod 2. J. L. Barnard's Australian material shows marked differences from the South African and Indian forms, especially as regards the shape of the palm of gnathopod 2 and the setification of the telson. Further sampling is necessary before it can be shown with certainty whether the various morphs so far described are synonymous or represent different species.

Mallacoota subcarinata (Haswell, 1880)

Elasmopus subcarinatus: Stebbing, 1910a: 458.

Maera subcarinata: K. H. Barnard, 1940: 460, fig. 26.

Mallacoota subcarinata: J. L. Barnard, 1972a: 247, figs 144, 145.

Records: SCD 262Q(2); LIZ 40C(3); MB 69R(1); 33°S/26°E/18–29 m (Stebbing 1910a).

Distribution: Mediterranean, Indo-Pacific.

Megaluropus agilis Hoek, 1889

Megaluropus agilis: Pillai, 1957: 50, fig. 10.

Records: MB 82H(1).

Diagnosis: Gnathopods simple; article 5 of gnathopod 2 dilated distally, article 6 tapering distally; peduncle of uropod 3 short, rami greatly flattened, subequal, their margins irregularly setose.

Distribution: North Atlantic, Mediterranean, India, South Africa.

Melita machaera K. H. Barnard, 1955

Melita machaera K. H. Barnard, 1955: 90–92, fig. 45.

Records: SCD 338T(1); TRA 54F(1).

Diagnosis: Lower margins of articles 4–6 of gnathopod 1 thickly fringed with short setae; palm of gnathopod 2 male slightly oblique, crenulate, a marked semicircular concavity at its centre, defining angle bearing two teeth and a pocket on its inner surface into which the tip of the dactyl closes; pleon segments 3 and 4 each with a small medio-dorsal tooth, segment 5 with a pair of latero-dorsal teeth; uropod 3 as long as pleon segments 2–6 together.

Distribution: Endemic to south coast of South Africa.

Melita orgasmos K. H. Barnard, 1940

Melita orgasmos K. H. Barnard, 1940: 454. Sivaprakasam, 1966: 114, fig. 12 k–m.

Records: SCD 104Y(1); KNY 171E; LLL 6D; K 8N; Still Bay, Port Elizabeth (K. H. Barnard 1940).

Distribution: India, southern Africa.

Melita zeylanica Stebbing, 1904

Melita zeylanica: J. L. Barnard, 1972a: 235, figs 139–141.

Records: SUN 8K(8); BMR 7J(1), BMR 23T(1), BMR 25H(1), BMR 26S(8); HAM 3R(3), HAM 9B(A), HAM 11G(P); HAV 3G, HAV 5D(1), HAV 7K(P), HAV 8D(C), HAV 9B, HAV 10E(C), HAV 18J(A); KNY 50D, KNY 112A, KNY 179C, KNY 291E; GBR 24G(2), GBR 46B(1); BRE 30Z(2), BRE 31E(3), BRE 43F(5), BRE 44V(6), BRE 52N(2), BRE 71L(3), BRE 128A(1), BRE 135A(20), BRE 135C(1), BRE 144B(1), BRE 146A(4); STJ 7R, STJ 15K(C), STJ 16J(C), STJ 26F(1), STJ 27H(C), STJ 29G, STJ 31U(A), STJ 32C; Little Brak River, Keurbooms River, Wilderness lagoon, George, Port Elizabeth, East London (K. H. Barnard 1940).

Distribution: Indo-Pacific (a brack-water species).

Pareiasmopus ? suluensis (Dana, 1853)

Pareiasmopus suluensis: Stebbing, 1888: 1029, pl. 100.

Records: QQ 4Y, S 54F.

Diagnosis: None of coxae 1–4 with antero-ventral teeth; palm of gnathopod 2 male oblique; article 2 of pereopods 3–5 not grossly serrate, articles 3–5 not very setose; pereon segment 7 and pleon segments 1–4 each with a pair of strong dorsal teeth; third pleonal epimeron strongly serrate ventrally.

Distribution: ? Indo-Pacific.

Remarks: Considerable controversy surrounds the identity of this form (for discussion see J. L. Barnard, 1972a: 253). The specimens described above conform with those of Stebbing (1888) but Stebbing's material differs from that of Dana (1853) in the presence of dorsal teeth on pereon segment 7 and in the

weaker serrations on article 2 of pereopods 3-5. Authors subsequent to Stebbing have further confused the situation by synonymizing his *P. suluensis* with *P. setiger* Chevreux, a move which it now appears was unjustified. As the situation stands at present, definitive identifications cannot be made until the existing forms are reviewed by someone who has access to the original types. In the meantime I feel I cannot go further than to associate my material with the well-known description of Stebbing (1888).

Family **Haustoriidae**

Bathyporeia sp.

Bathyporeia gracilis: K. H. Barnard, 1951: 704.

(non) *Bathyporeia gracilis* Sars 1891: 132-133, pl. 45 (1).

Records: SCD 244C(22), SCD 286H(2), SCD 329X(1), SCD 338M(1), SCD 349Q(1), SCD 370Q(1), SCD 376F(3), SCD 384R(1).

Distribution: Endemic, south coast of South Africa to South West Africa.

Remarks: This material was sent to Dr Wim Vader for use in a study on the status of *Bathyporeia gracilis* Sars, but was found by him to be an undescribed species (Vader 1970) which he is in the process of describing.

Cunicus n. gen.

Diagnosis: Antenna 1 geniculate between articles 2 and 3; antenna 2 geniculate between articles 3 and 4 and 4 and 5; mandibular palp not arising from basal process, molar represented by a spinose process; outer plate of maxilla 2 not enlarged; maxillipedal palp 4-articulate; coxae 1 and 2 rounded-quadrate, of moderate size; gnathopods subchelate, article 5 much longer than 6; pereopods with dactyls; uropods 1 and 2 represented by rounded setose lobes; uropod 3 biramous, rami subequal, the outer bi-articulate; telson cleft.

Type species: *Cunicus profundus* n. sp.

Relationships: This new genus lies closest to *Urothoe* but is distinguished from it by the reduced first and second uropods (these are biramous in *Urothoe*), the geniculate antennae and the unusual mandibular molar.

Cunicus profundus n. sp.

Figs 8, 9

Description of male (3.5 mm): Body not more than three times as long as wide; head as long as first two pereon segments, eyes absent; antennae short, subequal, held in life in a folded position along side of head; articles 1 and 2 of antenna 1 equal, setose dorsally (Fig. 8B), article 3 somewhat shorter than 2, joint

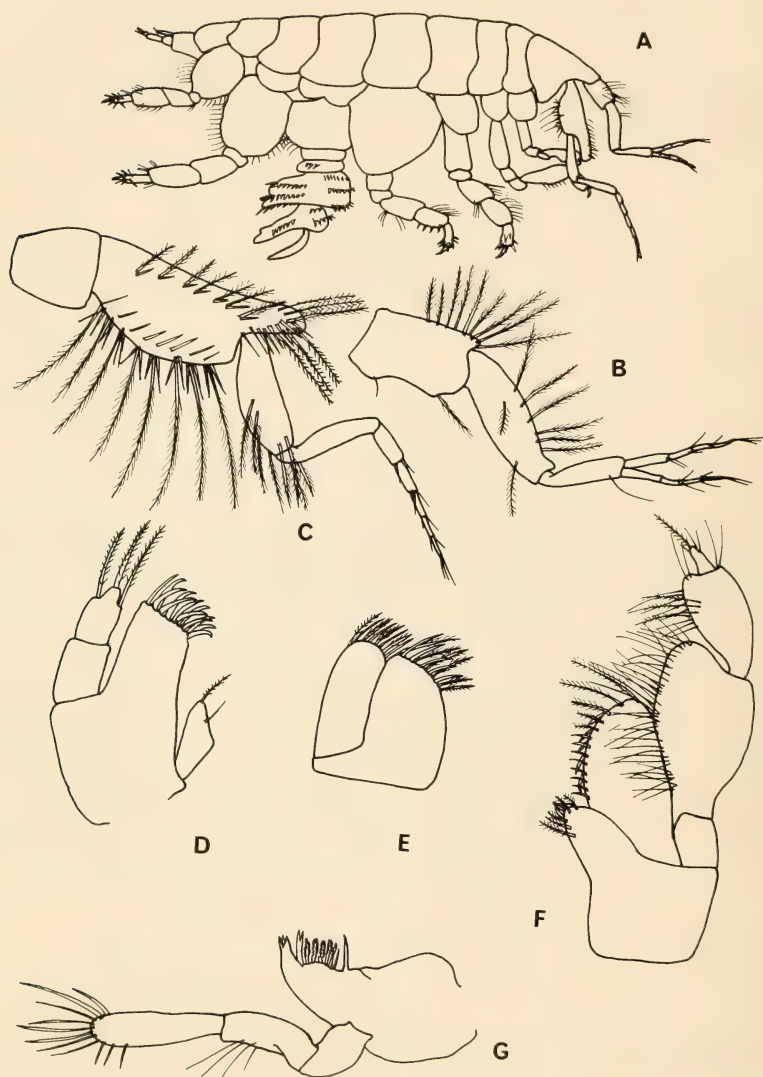


Fig. 8. *Cunicus profundus* n. gen., n. sp.
Male, 3,5 mm: A—lateral view; B—antenna 1; C—antenna 2; D—maxilla 1;
E—maxilla 2; F—maxilliped; G—mandible.

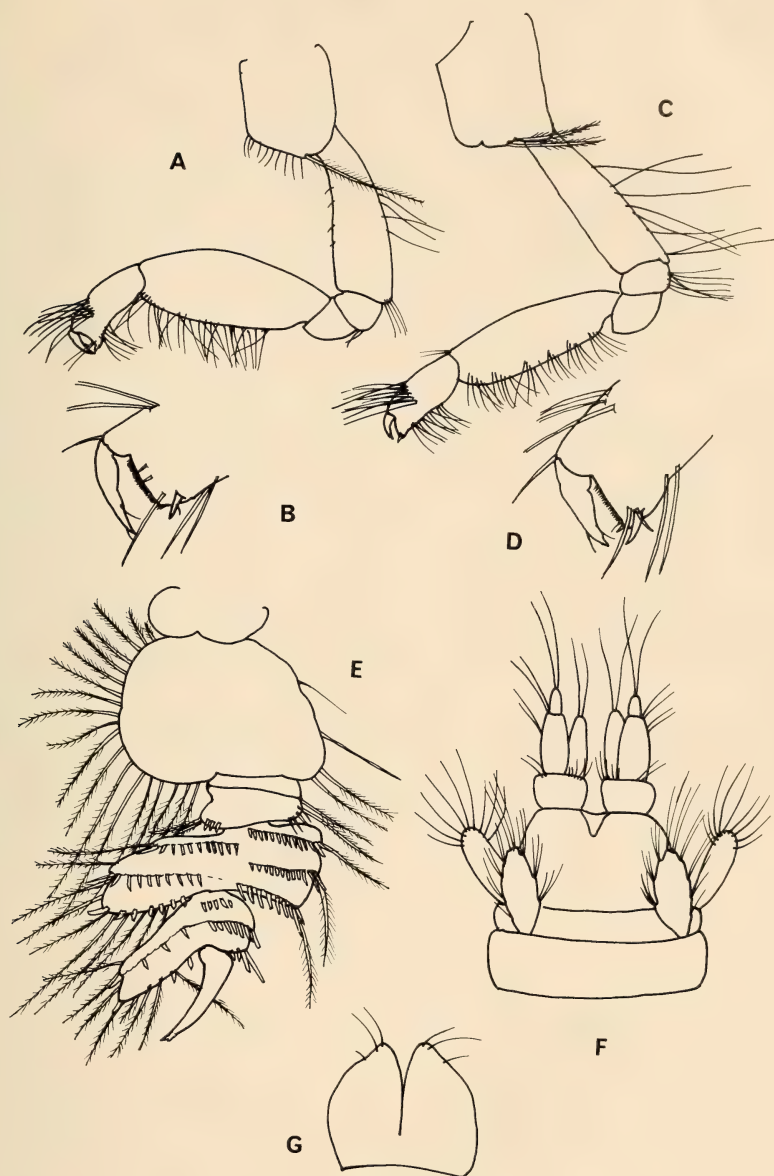


Fig. 9. *Cunicus profundus* n. gen., n. sp.
Male, 3,5 mm: A—gnathopod 1; B—palm of gnathopod 1 enlarged; C—gnathopod 2; D—palm of gnathopod 2 enlarged; E—pereopod 3; F—ventral view of urosome; G—telson.

between articles 2 and 3 geniculate, flagellum equal to accessory flagellum, both 4-articulate; antenna 2 geniculate between articles 3 and 4 and 4 and 5, peduncle setose and spinose (Fig. 8C), flagellum 5-articulate; mandible (Fig. 8G) with 3-articulate palp, incisor tridentate, lacinia mobilis bifid, spine row of six serrate spines, molar represented by a spiniform process; palp of maxilla 1 bi-articulate (Fig. 8D), tipped by three plumose setae, outer plate bearing 12 strong spines, inner plate with two short setae; plates of maxilla 2 (Fig. 8E) terminating in a row of alternating simple and plumose setae; maxilliped (Fig. 8F) with 4-articulate palp, outer plate with five distal plumose setae and a medial row of alternating spines and setae, inner plate terminating in a group of spines surrounded by short plumose setae.

Coxae rounded, 1-4 successively larger, distally setose, coxa 4 extending to tip of article 2 of pereopod 2; gnathopods 1 and 2 (Fig. 9A-D) subchelate, palms minutely pectinate, transverse, defined by large spines; pereopods 1 and 2 each with article 5 posteriorly spinose, dactyl basally surrounded by a ring of spines; pereopod 3 (Fig. 9E) greatly widened and strongly spinose, article 2 fringed by long plumose setae, article 4 with a fascicle of plumose setae arising from its inner margin, article 5 twice as wide as long and with three transverse rows of short strong spines and a marginal row of plumose setae on posterior lobe, article 6 greatly produced postero-distally into a spinose and setose lobe overhanging the simple cultriform dactyl; pereopods 4 and 5 with plumose setae on posterior margin of article 2 and a ring of strong spines around base of dactyl.

Pleon somewhat narrower than pereon, pleonal epimera postero-distally rounded, the second with a fascicle of plumose setae on its external surface; urosome very short (Fig. 9F), uropods 1 and 2 represented only by rounded setose lobes; uropod 3 of normal structure, peduncle quadrate, outer ramus bi-articulate, slightly longer than the inner; telson cleft, extending to centre of rami of uropod 3, apex of each lobe with three small setae.

Female: Ovigerous at 3,5 mm, bearing 3-5 large eggs, otherwise similar to male.

Holotype: SAM A13212, male, 3,5 mm.

Type Locality: SCD 384P, 33°52'S/25°38'E, 15 December 1962, depth 7 m, substrate grey sand.

Material: SCD 83B(1), SCD 128 U(1), SCD 225F(2), SCD 285P(1), SCD 286F(1), SCD 350M(1), SCD 370P(1), SCD 384P(1).

Remarks: The body form of this species and the fact that it has been recovered from depths of up to 0,6 m beneath the sand surface bear witness to its extraordinary degree of adaptation to the fossorial mode of life. Morphological adaptations include the broadly truncated body shape, wide pereopods, large coxae, reduced urosome and the loss of eyes. Other features also considered advanced include the minimal degree of sexual dimorphism and small number

of eggs carried by the female (3–5). These factors taken together indicate that *Cunicus* is probably the most advanced burrowing amphipod known, certainly the tendency for reduction of urosome and broadening of pereon are taken to their extreme here.

Urothoe coxalis Griffiths, 1974

Urothoe coxalis Griffiths, 1974b: 238, fig. 5.

Records: KNY 157B(9).

Distribution: Endemic, Durban to Knysna.

Urothoe elegans Bate, 1857

Urothoe elegans: Chevreux & Fage, 1925: 101, fig. 95.

Records: SCD 232F(1), SCD 392T(1); SST 5E(3), SST 16H(1), SST 19E(1), SST 24J(4); 34°S/22°E/81 m (K. H. Barnard 1955).

Distribution: Atlantic and Indian Oceans.

Urothoe grimaldi Chevreux, 1895

Urothoe grimaldii: Chevreux & Fage, 1925: 99, fig. 93. K. H. Barnard, 1955: 84, fig. 41B.

Records: SCD 122D(1), SCD 135G(1), SCD 141M(7), SCD 146B(1), SCD 198L(95), SCD 202C(1), SCD 222N(1), SCD 225E(7), SCD 230C(1), SCD 232E(2), SCD 257N(14), SCD 267J(5), SCD 276L(10), SCD 278L(2), SCD 286D(10), SCD 315X(24), SCD 329V(8), SCD 348Z(4), SCD 368(T)1, SCD 370N(7), SCD 376G(13), SCD 381R(8); SST 1G(1), SST 61N(2), SST 73G(1); MB 71H(6); 34°S/22°E/110 m, 34°S/22°E/81 m (K. H. Barnard 1955).

Distribution: Atlantic, Mediterranean, India, South Africa.

Urothoe platypoda n. sp.

Fig. 10

Description of male (2.5 mm): Head as long as three pereon segments; eyes large, dark, subcircular; flagellum of antenna 1 5-articulate, accessory flagellum of two equal segments; antenna 2 as long as body (Fig. 10A), terminal article of peduncle bearing five large calceoli, flagellum slender, 26-articulate; palp of maxilla 1 bi-articulate, outer plate bearing 10 strong spines; mandible (Fig. 10B) with large quadrate molar and 3-articulate palp, article 1 of palp shorter than 2 or 3; maxilliped (Fig. 10C) with 4-articulate palp, article 2 broadly expanded medio-distally, the expansion strongly setose, article 3 widening distally, outer plate twice length of inner, bearing five strong spin-teeth medially, inner plate terminating in five curved spines and a few short plumose setae.

Coxa 1 tapering to an acute apex, coxae 2–4 slightly produced backwards,

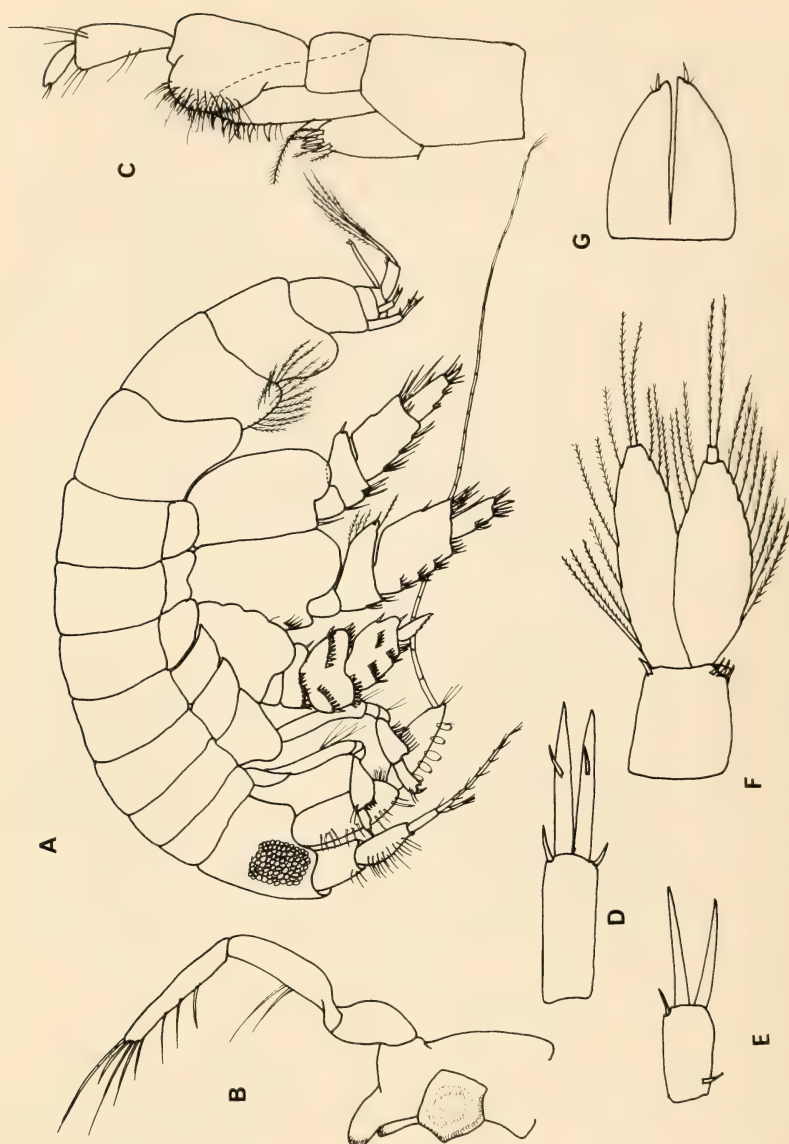


Fig. 10. *Urothoe platypoda* n. sp.

Male, 2,5 mm: A—lateral aspect; B—mandible; C—maxilliped; D—uropod 1; E—uropod 2; F—uropod 3; G—telson.

remaining coxae rounded; gnathopod 1 simple, article 5 expanded posteriorly, bearing four spines postero-distally, article 6 small; gnathopod 2 subchelate, palm strongly concave; pereopods 1 and 2 strongly spinose posteriorly, dactyls present; article 2 of pereopod 3 unusually large, posterior margin scalloped, postero-distal corner lobed to obscure part of article 3, article 4 with a single postero-distal spine and a row of nine antero-distal spines, article 5 somewhat broader than long, bearing two transverse rows of ten and nine spines anteriorly and two rows of nine and six spines posteriorly (Fig. 10A), article 6 with three

anterior rows of seven, five and three spines, a central group of five spines and two single spines on posterior margin, dactyl broad, anteriorly serrate; article 2 of pereopods 4 and 5 large, lobed postero-distally, articles 4 and 5 strikingly broadened, 4 being as wide as 2.

Pleon segments very large, pleonal epimera postero-distally rounded, the second bearing plumose setae on its outer surface; rami of uropod 1 (Fig. 10D) equal, peduncle with two distal spines and each ramus with a single large spine mid-dorsally; uropod 2 (Fig. 10E) much shorter than 1, peduncle with one proximal and one distal spine, rami naked; uropod 3 (Fig. 10F) with quadrate peduncle, rami foliaceous, subequal, bearing long marginal plumose setae, outer ramus with a short article 2; telson (Fig. 10G) 1.5 times as long as peduncle of uropod 3, cleft to base, each lobe bearing a single spine and a minute seta at its apex

Female (3 mm): Similar to the male except for the eyes, second antennae and third uropods. The eyes are much smaller than those of the male, being composed of about 12 well-spaced ommatidia, while antenna 2 is subequal to antenna 1, lacks calceoli and has a 2-articulate flagellum. The third uropods do not exceed the tip of the telson and have fewer, shorter marginal setae.

Holotype: SAM A13210, male, 2.5 mm.

Type locality: SCD 391G, 34°05'S/23°24'E, 8 December 1962, depth 11 m, substrate yellow sand.

Relationships: The shape of pereopods 3–5 serves to diagnose this species. The second articles (especially that of pereopod 3) are unusually large and the enlarged flattened articles 4 and 5 of pereopods 4 and 5 are unique in the genus.

Material: SCD 202D(6), SCD 230B(1), SCD 349N(1), SCD 391G(12).

Urothoe pinnata K. H. Barnard, 1955

Urothoe pinnata K. H. Barnard, 1955: 86, fig. 42.

Records: SCD 288G(1); SST 52N(5), SST 54B(2), SST 56P(3).

Distribution: Endemic, Natal to False Bay.

Urothoe pulchella (Costa, 1853)

Urothoe pulchella: Chevreux & Fage, 1925: 99, fig. 92. K. H. Barnard, 1955: 83, fig. 41A.

Records: SCD 74A(1), SCD 83A(2), SCD 104T(1), SCD 128S(2), SCD 135F(20), SCD 148H(16), SCD 173W(1), SCD 202B(2), SCD 211V(3), SCD 285Q(6), SCD 286E(1), SCD 287D(1), SCD 333R(4), SCD 345U(19), SCD 348Y(1), SCD 349M(10), SCD 350L(1), SCD 383P(9), SCD 384N(45), SCD 391H(19); SST 1E(2), SST 9B(2), SST 32C(1), SST 34H(3), SST 56U(3), SST 59K(3), SST 60J(8), SST 61M(3), SST 62N(1), SST 63Q(1), SST 65E(9), SST 67M(4),

SST 74D(1), SST 76M(1), SST 77D(7), SST 78D(5); MB 82C(2); SUN 5D(10); HAV 7M, HAV 13L(2), HAV 17B(A); KNY 187B(3); GBR 12C(45), GBR 16J(7); STJ 14C(C), STJ 15L(P), STJ 16U(1), STJ 17C(1); 34°S/22°E/109 m (K. H. Barnard 1916); 34°S/22°E/77 m, 34°S/22°E/110 m (K. H. Barnard 1955).

Distribution: Mediterranean, Atlantic, South Africa.

Urothoe tumorosa Griffiths, 1974

Urothoe tumorosa Griffiths, 1974b: 241, fig. 6.

Records: SST 54C(2).

Distribution: Endemic, Durban to Still Bay.

Family **Ischyroceridae**

Ischyrocerus anguipes Kröyer, 1838

Ischyrocerus anguipes: J. L. Barnard, 1954: 35, pls 32, 33; 1969b: fig. 107B.

Records: SS 55L.

Distribution: Cosmopolitan in tropical and temperate seas.

Jassa falcata Montagu, 1808

Jassa falcata: Sexton & Reid, 1951: 30–47, pls 4–30. J. L. Barnard, 1969a: 115, figs 38, 39.

Records: MB 21E(1); KNY 166D, KNY 176C(A), KNY 179E(1); J 11K; L 458A; E 234; ZZ 3N; T 13L; VV 2J; AR 1R(1).

Distribution: Cosmopolitan.

Parajassa chikoa n. sp.

Fig. 11

Description of male (2,5 mm): Head as long as three pereon segments, ocular lobes moderately produced, distally rounded, eyes round; antenna 1 slightly shorter than pereon, articles 2 and 3 subequal, 1,5 times as long as 1, flagellum 4-articulate, accessory flagellum not seen, presumed vestigial; mandible (Fig. 11B) with large 3-articulate palp, article 1 shorter than 2, 2 equal to 3, 3 strongly setose distally, cutting edge of five strong teeth, lacinia mobilis apically bifurcate, spine row of two strong spines, molar large, tritulative; outer lobes of lower lip simple, neither notched nor excavate; maxilla 1 (Fig. 11D) bearing bi-articulate palp, distal article ending in five serrate blade-spines and three subterminal plumose setae, outer plate bearing seven strong serrate spines, inner plate simple; maxilliped (Fig. 11E) with 4-articulate palp, outer plate bearing seven medio-distal spines, inner plate with an oblique row of plumose setae and three small distal spines.

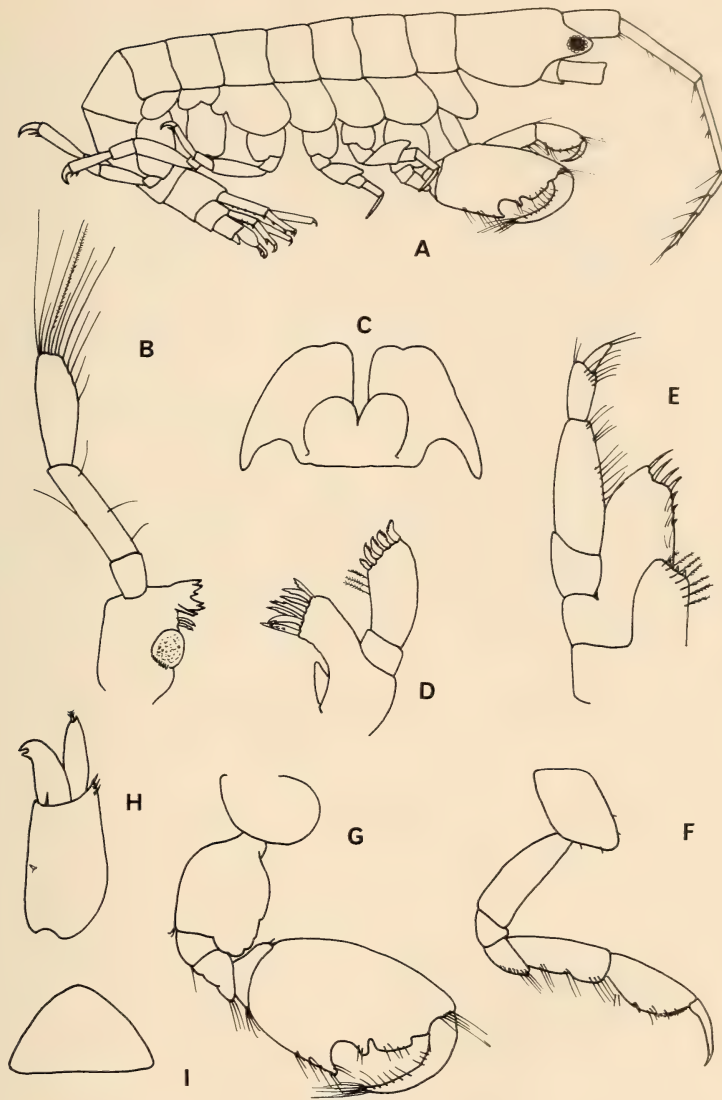


Fig. 11. *Parajassa chikoa* n. sp.

Male, 2,5 mm: A—lateral aspect; B—mandible; C—lower lip; D—maxilla 1; E—maxilliped; F—gnathopod 1; G—gnathopod 2; H—uropod 3; I—telson.

Coxae 1-4 rounded, subequal, 5 bilobed, 6 and 7 each half as long as 5; gnathopod 1 (Fig. 11F) subchelate, palm pectinate, defined by a single small spine, dactyl slightly exceeding palm; gnathopod 2 (Fig. 11G) powerfully subchelate, article 2 distally lobed, the lobe extending proximally as an anterior keel, 5 cup-shaped, embracing the very large article 6, palm oblique, subequal to hind margin, bearing a flat-topped tooth near finger hinge, a conical tooth proximal to it then a strong semicircular concavity preceding the defining tooth, dactyl moderately thickened, bearing a row of small setae posteriorly and a fascicle of long setae at its apex; article 4 of pereopods 1 and 2 with antero-distal corner expanded, dactyl long, slender; article 2 of pereopod 3 subcircular, article 6 bearing a distal spine; pereopods 4 and 5 somewhat larger than 3 but of similar structure.

Pleon and urosome flexed beneath pereon; pleonal epimera rounded; urosomal segments subequal in length, uropods 1-3 extending equally; peduncle of uropod 1 with five dorsal spines, inner ramus slightly exceeding outer, each with a strong apical spine, outer ramus also with three dorsal spines; peduncle of uropod 2 with three dorsal spines, each ramus with two dorsal and a terminal spine, inner ramus slightly longer than outer; peduncle of uropod 3 (Fig. 11H) twice length of rami, inner ramus tapering evenly, apex bearing a single minute seta, outer ramus terminally upturned to form a pair of non-articulate hooks (one specimen showed three hooks on the one uropod 3 and two on the other); telson triangular, entire, smooth.

Holotype: SAM A13218, male, 2.5 mm.

Type locality: SCD 99M; 34°33'S/24°01'E, 21 July 1959, depth 130 m, substrate rock.

Relationships: Of the four existing species in this genus *Parajassa pelagica* Leach differs from *P. chikoa* n. sp. by virtue of its minute 2-articulate flagellum of antenna 1, while *P. angularis* Shoemaker has distinctive setose first and second uropods. The other two species, *P. tristanensis* (Stebbing) and *P. gorgoniana* (Schellenberg) are closely allied to *P. chikoa* n. sp. but have only a single tooth on the palm of gnathopod 2 and smaller hooks on the outer ramus of uropod 3.

Material: SCD 99M(1), SCD 343Z(1). (Both ♂♂).

Family Leucothoidae

Leucothoe ctenochir K. H. Barnard, 1925

Leucothoe ctenochir K. H. Barnard, 1925: 342, pl. 34, fig. 8.

Records: SCD 93N(2), SCD 159W(15), SCD 172S(2); MB 13M(1), MB 23J(1), MB 28H(1), MB 54U(1).

Distribution: Endemic to east coast of South Africa.

Leucothoe dolichoceras K. H. Barnard, 1916

Leucothoe dolichoceras K. H. Barnard, 1916: 157, pl. 26, fig. 14.

Records: SCD 181R(1); SST 11R(1); 34°S/25°E/137 m, 32°S/28°E/93 m (K. H. Barnard 1916).

Distribution: Endemic, Natal to west coast of South Africa.

Leucothoe richiardi Lessona, 1865

Leucothoe richiardi: K. H. Barnard, 1916: 150.

Leucothoe richiardi: Sivaprakasam, 1967b: 385, fig. 2.

Records: SCD 24M(2), SCD 131X(1), SCD 159Q(1), SCD 181Q(1), SCD 204U(1), SCD 244F(1), SCD 310E(1), SCD 353H(1); SST 9D(1), SST 11Q(18); SST 19D(1), SST 24F(2), SST 29B(2), SST 37V(1); MB 23F(4), MB 40F(1); 34°S/25°E/138 m, 33°S/28°E/121 m (K. H. Barnard 1916).

Distribution: Mediterranean, India, South Africa.

Leucothoe spinicarpa (Abildgaard, 1789)

Leucothoe spinicarpa: Sivaprakasam 1967b: 384, fig. 1.

Records: SCD 41R(2), SCD 95E(1), SCD 115D(1), SCD 172T(12), SCD 198X(1), SCD 253F(1), SCD 300U(1), SCD 302W(1), SCD 366M(3), SCD 366W(1); LIZ 37P(3), LIZ 40A(1); MB 23X(2), MB 50P(3), MB 54U(8), MB 69T(1); TRA 55W(1); LLL 6W; 32°S/28°E/174 m, 33°S/28°E/91 m (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Family **Liljeborgiidae***Liljeborgia consanguinea* Stebbing, 1888

Liljeborgia consanguinea Stebbing, 1888: 980, pl. 91.

Records: 35°S/20°E/565 m (Stebbing 1910a).

Diagnosis: Each of pleon segments 1–5 produced into a small but distinct mid-dorsal tooth; coxae 1–3 each with a denticle at both distal corners, coxa 4 serrate posteriorly; pleonal epimera 1 and 2 postero-distally produced into a small point, that of third pleonal epimeron larger and upturned with a small sinus above; telson 60% cleft, a single spine at apex of each lobe; palm of gnathopod 2 male smooth.

Distribution: Antarctica, southern Indian Ocean.

Liljeborgia dubia (Haswell, 1880)

Eusirus dubius Haswell, 1880: 331, pl. 30, fig. 3.

Records: SCD 24R(3), SCD 120C(1), SCD 216E(1), SCD 349S(1), SCD 353R(1), SCD 366R(3); SST 5H(1), SST 9G(1), SST 16R(5), SST 18X(1).

Diagnosis: Pleon segments 1 and 2 each with five dorsal teeth, 3 with a minute tooth between two rounded lobes, 4 and 5 each with a strong carinate dorsal tooth; coxa 4 with two teeth on hind margin; postero-distal corner of third pleonal epimeron acute, slightly upturned; telson cleft nearly to base, a long spine in a notch at apex of each lobe; palm of gnathopod 2 male with an acute distal tooth.

Distribution: Australia, New Zealand, South Africa.

Liljeborgia epistomata K. H. Barnard, 1932

Liljeborgia epistomata K. H. Barnard, 1932: 144, fig. 83; 1955: 89, fig. 44.

Records: SCD 110W(1), SCD 135M(1), SCD 141P(4), SCD 222J(1), SCD 225L(1), SCD 376K(1).

Distribution: Endemic, Natal to Saldanha Bay.

Liljeborgia kinahani (Bate, 1862)

Liljeborgia kinahani: Chevreux & Fage, 1925: 157, fig. 157.

Records: SCD 262K(1), SCD 356K(1); MB 23H(2), MB 87F(3).

Diagnosis: Pleon segments 1 and 2 dorsally tridentate, 3 smooth, 4 and 5 each with a single dorsal tooth; coxae 1–3 without distal teeth; coxa 4 not serrate posteriorly; pleonal epimera 1 and 2 postero-distally produced into a minute tooth, third pleonal epimeron with a small sinus above postero-distal tooth; telson cleft nearly to base, lobes divergent, a long spine arising from a notch in apex of each lobe; palm of gnathopod 2 male smooth.

Distribution: North Atlantic, South Africa.

Liljeborgia palmata n. sp.

Fig. 12

Description of male (6 mm): Head as long as first two pereon segments, rostrum acute, slightly downturned, half length of article 1 of antenna 1, eyes absent; antenna 1 as long as peduncle of antenna 2, article 1 considerably longer than 2 plus 3, flagellum 19-articulate, twice length of peduncle, accessory flagellum 10-articulate; flagellum of antenna 2 14-articulate, as long as terminal article of peduncle; mandible (Fig. 12A) with 3-articulate palp, articles 1 and 2 subequal, longer than 3, primary cutting edge with three large teeth and numerous serrations, secondary cutting edge of five large teeth, spine row of eight spines, molar redundant, represented by a few spines; inner plate of maxilla 1 tipped by a single seta, outer plate bearing eight long pectinate spines, palp bi-articulate with eight small spines lining inner edge and four small setae along outer margin; plates of maxilla 2 subequal; inner plate of maxilliped bearing five terminal setae, outer plate with a row of seven medial spines and seven submarginal setae, palp 4-articulate.

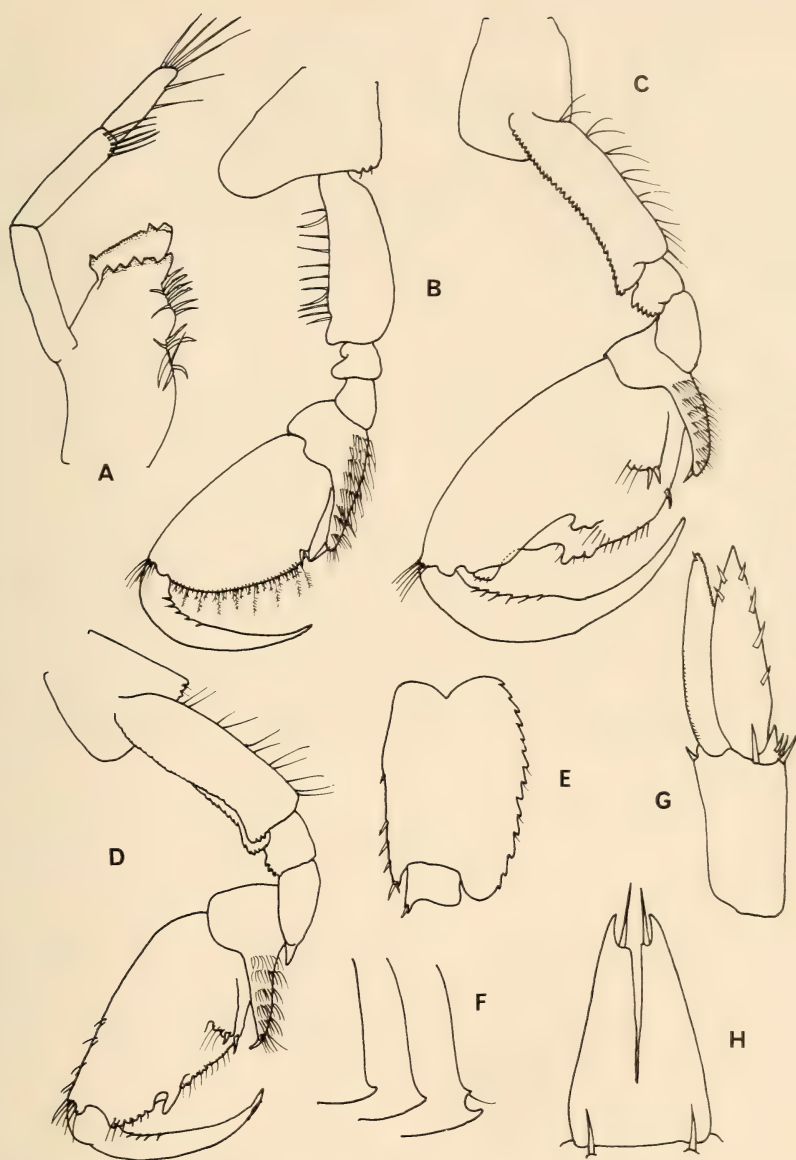


Fig. 12. *Liljeborgia palmata* n. sp.
 Male, 6 mm: A—mandible; B—gnathopod 1; D—gnathopod 2; E—articles 2 and 3 of pereopod 5; F—pleonal epimera 1-3; G—uropod 3; H—telson.
 Male, 10 mm: C—gnathopod 2 (inner aspect).

Coxae 1 and 2 each bearing two small postero-distal notches; gnathopod 1 (Fig. 12B) with a row of setae along anterior margin of article 2, articles 2 and 3 antero-distally lobed, 5 produced to protect 6 posteriorly, palm evenly convex, bearing alternating long and short setae, defined by two spines, dactyl bearing five proximal teeth; gnathopod 2 (Fig. 12D) larger than 1, article 2 bearing two serrate anterior keels which are distally produced into moderate lobes, article 3 with an antero-distal serrate lobe, article 6 tapering off from defining angle, palm irregularly toothed and varying greatly with age (Fig. 12C, D), dactyl with 4-6 proximal teeth, closing between defining spine and a spinose ridge arising from inner face of article 6; pereopods 1 and 2 slender; article 2 of pereopods 3-5 widened, posteriorly serrate, the serrations most marked on pereopod 5, where they number 14.

Pleonal tooth formula 1:1:0:1:1, the teeth on the first two segments appressed while those on segments 4 and 5 form carinae; postero-distal corner of pleonal epimera 1 and 2 produced into a small tooth, third pleonal epimeron with a semicircular concavity above postero-distal tooth and a second tooth bearing a single small seta above this (Fig. 12F); uropods extending about equally, peduncle of uropod 1 with a terminal spine, outer ramus marginally the shorter; uropod 2 with two dorsal spines on peduncle, outer ramus slightly the shorter; rami of uropod 3 (Fig. 12G) subequal, the outer naked but minutely pectinate on upper margin, the inner with four dorsal and two ventral spines; telson (Fig. 12H) 80% cleft, each lobe bearing a single strong seta in a subapical notch.

Female: Differing from the male only in the possession of brood plates and in the structure of gnathopod 2, which is slightly larger than gnathopod 1, but of the same structure.

Holotype: SAM A13221, male, 6 mm.

Type locality: SST 29G, 34°40'S/21°39'E, 21 June 1972, depth 80 m, substrate coarse shelly sand.

Relationships: Males of this species can easily be distinguished by the unusual shape of the palm of gnathopod 2 and by the serrate articles 2 and 3 of gnathopod 2. The female is similar to that of *Liljeborgia hansonii* Hurley, which is unfortunately known only from the female. However, Hurley describes his species as bearing red-brown eyes, whereas *L. palmata* n. sp. has no eyes.

Material: SST 16S(4), SST 29G(2).

Listriella sinuosa n. sp.

Fig. 13

Description of male (8 mm): Head only slightly longer than first pereon segment, postantennal angle smoothly rounded, eyes small, round, black; antenna 1 shorter than peduncle of antenna 2, articles 1 and 2 subequal, 3 very short,

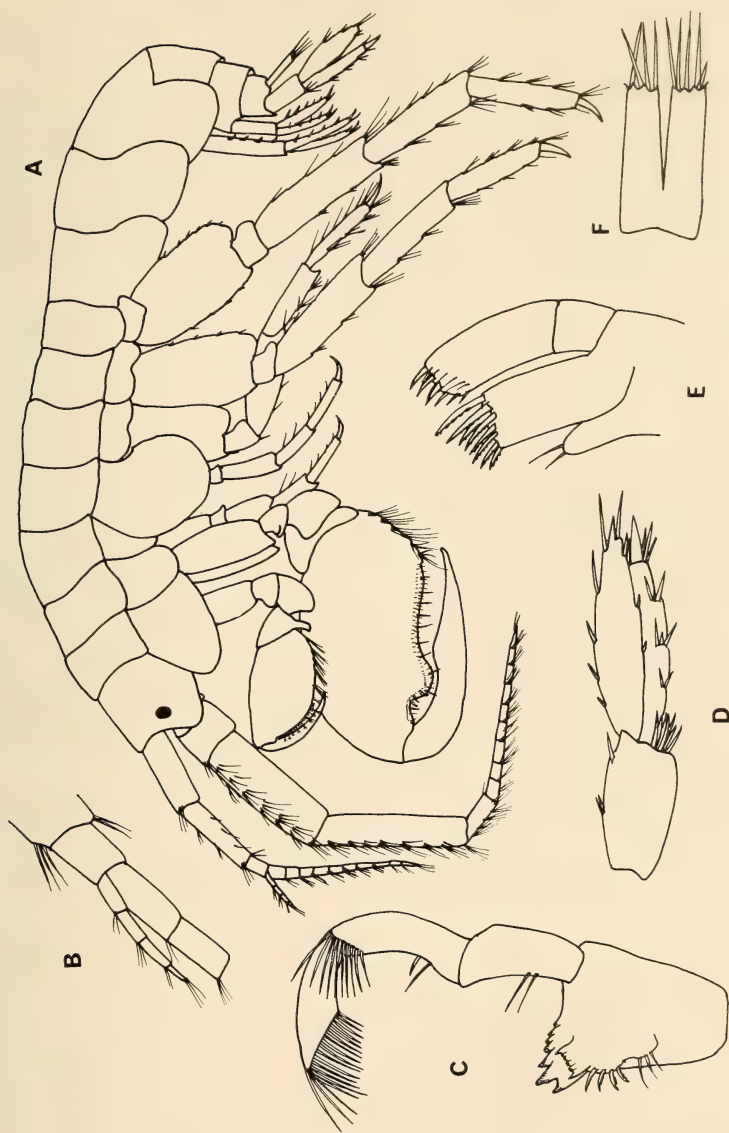


Fig. 13. *Listriella sinuosa* n. sp.

Male, 8 mm: A—lateral aspect; B—accessory flagellum; C—mandible; D—uropod 3; E—maxilla 1; F—telson.

flagellum 10-articulate, accessory flagellum (Fig. 13B) 4-articulate; antenna 2 as long as pereon, flagellum 10-articulate; mandible (Fig. 13C) with broad 3-articulate palp, articles 2 and 3 bearing rows of strong setae distally, incisor strongly chitinized, primary cutting edge with seven strong teeth, spine row of four spines, molar degenerate, represented by three setae; maxilla 1 (Fig. 13E) with two apical setae on inner plate and eight strong pectinate spines on outer plate, palp bi-articulate, tipped by three short spines and a row of short setae;

inner plate of maxilliped with three setae along inner margin and a spine and two setae at apex, outer plate with seven graduated spines along medial margin and three setae distally, palp 4-articulate.

Coxa 1 produced anteriorly, coxae 2 and 3 rounded, 4 nearly twice as long as 3, excavate posteriorly; gnathopod 1 much smaller than 2, palm evenly convex, lined with alternating long and short setae; gnathopod 2 very large, article 2 with two anterior keels, palm very long, bearing three small spines on a rounded convexity near finger hinge, otherwise bearing scattered short setae; pereopods 1 and 2 slender; article 2 of pereopods 3–5 widened; pereopods 4 and 5 very elongate, hind margins of article 2 feebly serrate.

Pleonal epimera all smoothly rounded postero-distally; uropod 1 with a row of about five dorsal peduncular spines, rami equal, spinose dorsally and apically; uropod 2 without peduncular spines, otherwise resembling uropod 1; uropod 3 (Fig. 13D) extending well beyond 1 and 2, peduncle bearing three dorsal and several ventral spines, rami subequal, the outer with a spiniform second article; telson (Fig. 13F) 80% cleft, each lobe bearing four large spines, a smaller spine and a minute seta across its truncated apex.

Holotype: SAM A13215, male, 8 mm, unique.

Type locality: SST 41P, 34°25'S/21°28'E, 21 June 1972, depth 50 m, substrate green mud.

Relationships: All other species in this genus, with the exception of *L. lindae* Griffiths, have a bi-articulate accessory flagellum. *L. sinuosa* can be distinguished from *L. lindae* by virtue of its smoothly rounded pleonal epimera and strongly setose telson, as well as by the structure of gnathopod 2.

Family Lysianassidae

Amaryllis macrophthalma Haswell, 1880

Amaryllis macrophthalma: J. L. Barnard, 1972a: 262–269, figs 156–158.

Records: SCD 172X(5), SCD 181L(1), SCD 198C(3), SCD 204W(3), SCD 227S(2), SCD 244Q(3), SCD 266S(3), SCD 300V(2), SCD 321V(1), SCD 379K(29); SST 16V(7), SST 29M(1); LIZ 17G(1), LIZ 29N(1), LIZ 37M(2); MB 16D(1), MB 20U(1), MB 40H(1), MB 50Y(1), MB 66N(1), MB 73L(3); KNY 57C(C), KNY 171H; TRA 55X(1), TRA 58X(1); LLL 6G; E 231A; KKN 43E; 'Algoa Bay', 33°S/27°E/112 m (K. H. Barnard 1916); 33°S/26°E/18–29 m (Stebbing 1908a).

Distribution: Cosmopolitan in southern hemisphere.

Aristias symbiotica K. H. Barnard, 1916

Aristias symbiotica K. H. Barnard, 1916: 121.

Records: SCD 55C(14).

Distribution: Endemic, Moçambique to South West Africa.

Cyphocaris faurei K. H. Barnard, 1916

Cyphocaris faurei K. H. Barnard, 1916: 117, pl. 26, fig. 4.

Records: 33°S/28°E/450–550 m (K. H. Barnard 1916).

Diagnosis: First pereon segment greatly enlarged and swollen anteriorly but not projecting over head; coxa 4 anteriorly and distally strongly convex, posterior margin concave on either side of a medial tooth; article 2 of pereopod 3 produced posteriorly as a curved spiniform process which extends to tip of article 5, both margins of the process entire; telson as long as urosome, 75% cleft, apices entire, lacking spines.

Distribution: Cosmopolitan, bathypelagic.

Euonyx conicurus K. H. Barnard, 1955

Euonyx conicurus K. H. Barnard, 1955: 80, fig. 38.

Records: SCD 102G(1), SCD 160C(3).

Diagnosis: Eyes present; article 1 of antenna 1 prominently lobed distally; pleon segment 4 depressed at base then raised posteriorly into a large forward-directed triangular carina.

Distribution: Endemic to south coast of South Africa.

Hippomedon onconotus (Stebbing, 1908)

Tryphosa onconotus Stebbing, 1908: 65, pl. 35.

Records: SCD 104V(1), SCD 104W(1), SCD 106U(1), SCD 120D(2), SCD 202F(3), SCD 204V(1), SCD 211X(1), SCD 216N(22), SCD 225M(2), SCD 235U(5), SCD 343V(6), SCD 350N(1), SCD 391L(4), SCD 392S(5); SST 18Y(2), SST 24R(1), SST 62J(3), SST 63M(2), SST 65H(1), SST 67P(1), SST 68Q(3), SST 70P(1), SST 74E(1).

Distribution: Endemic to South Africa.

Ichnopus taurus Costa, 1853

Ichnopus macrobetomma Stebbing, 1917: 38, pl. 96 A.

Ichnopus taurus: Chevreux & Fage, 1925: 48, fig. 30.

Records: 33°S/27°E/91 m (K. H. Barnard 1916); 33°S/28°E/47 m (Stebbing 1917).

Diagnosis: Eyes very large; antennae slender; upper lip slightly produced in front of epistome; mandibular molar laminate, palp attached level with molar; gnathopod 1 simple, slender, dactyl strongly spinose posteriorly; dactyl of gnathopod 2 minute; gills plated on both sides; pereopod 5 much longer than 4; inner ramus of uropod 2 constricted; telson deeply cleft.

Distribution: Mediterranean, North Atlantic, South Africa.

Lepidepecreum twalae n. sp.

Fig. 14

Description of female (2,5 mm): Head dorsally shorter than first pereon segment, produced below antenna 1 into a large apically rounded lobe, eyes present but almost colourless in preserved animal; article 1 of antenna 1 (Fig. 14B) laterally flattened but not dorsally carinate, almost as tall as head, articles 2 and 3 much smaller, flagellum 5-articulate, shorter than peduncle, accessory flagellum small, bi-articulate; antenna 2 (Fig. 14C) not much longer than 1, article 3 elongate, flagellum 3-articulate, about as long as terminal article of peduncle; mandible (Fig. 14D) with smooth incisor, spine row of three spines, molar setulose, of moderate size, palp 3-articulate, attached proximal to molar, article 2 very elongate, article 3 finely setulose throughout and bearing three lateral and three terminal setae; maxilla 1 (Fig. 14E) with bi-articulate palp, article 2 terminating in 6 blade spines and a small seta, outer plate bearing ten powerful serrate spines, inner plate with two setae at its tip; plates of maxilla 2 (Fig. 14F) subequal; maxilliped (Fig. 14G) with 4-articulate palp, outer plate bearing 12 nodular spines along medial margin and an oblique row of five larger spines submarginally, inner plate with two distal spines and six medial plumose setae.

Pereon dorsally smooth, coxae 1–4 all visible, elongate and distally touching their partners on the opposite side, coxa 4 excavate posteriorly, 5–7 subcircular; gnathopod 1 (Fig. 14I) subchelate, palm transverse, defined by two large spines, dactyl with accessory tooth; gnathopod 2 (Fig. 14H) chelate, article 5 slightly longer than 6, both distally setulose; article 2 of pereopods 1 and 2 slender; article 2 of pereopods 3–5 rotund, article 4 produced into a postero-distal lobe.

Pleon segments 1–3 dorsally smooth, pleonal epimera postero-distally rounded; pleon segment 4 bearing a large dorsal triangular carina; uropods 1–3 all projecting equally; uropod 3 (Fig. 14K) with equal rami, inner ramus with three large spines on dorsal margin, outer ramus with two spines at apex of article 1, article 2 triangular, tapering evenly; telson (Fig. 14L) twice as long as wide, 70% cleft, each lobe tipped by a small spine and with a short mid-dorsal plumose seta.

Holotype: SAM A13220, female, 2,5 mm, unique.

Type locality: SCD 343W, 36°39'S/23°41'E, 11 February 1962, depth 121 m, substrate shelly sand.

Relationships: This species can be distinguished from most others in the genus by the lack of carinae on the pereon and on article 1 of antenna 1. These features are also absent in *Lepidepecreum typhlops* Bonnier and *L. cingulatum* K. H. Barnard, but of these the former lacks eyes and the latter does not have a carina on the fourth pleon segment.

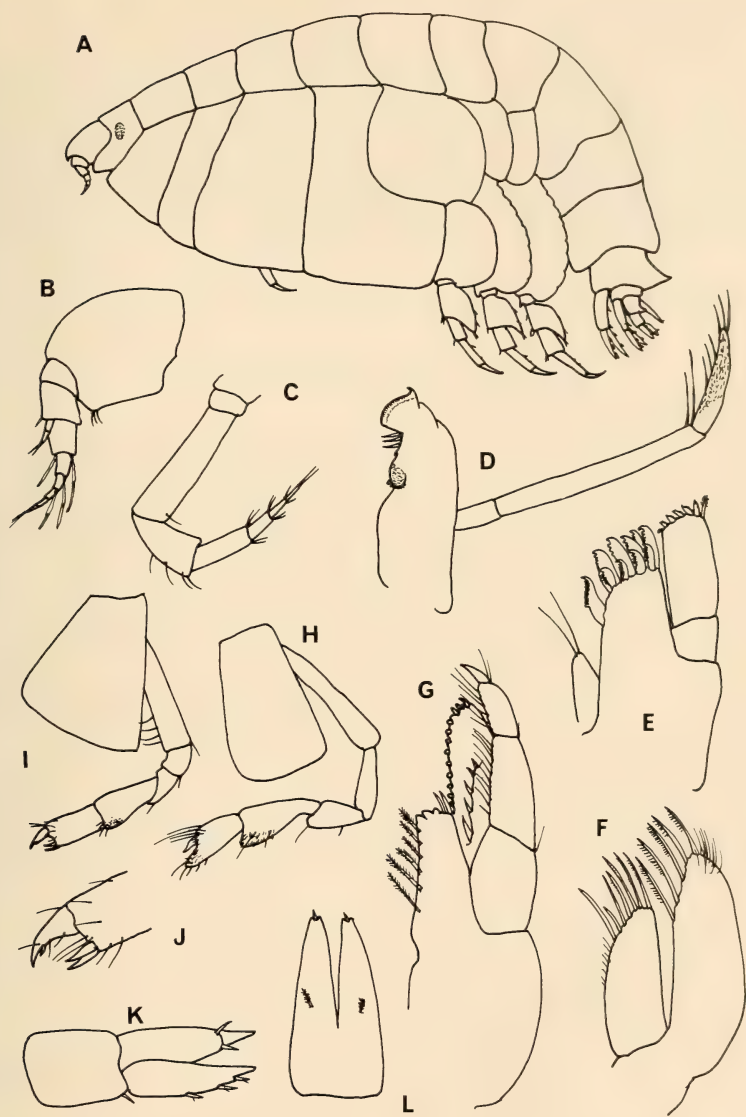


Fig. 14. *Lepidepocentrum twalae* n. sp.

Female, 2,5 mm: A—lateral aspect; B—antenna 1; C—antenna 2; D—mandible;
E—maxilla 1; F—maxilla 2; G—maxilliped; H—gnathopod 2; I—gnathopod 1;
J—enlargement of palm of gnathopod 1; K—uropod 3; L—telson.

Lysianassa ceratina (Walker, 1889)

Lysianassa cubensis: K. H. Barnard, 1916: 120.

Lysianassa ceratina: Chevreux & Fage, 1925: 42, fig. 23.

Records: SCD 160D(9), SCD 173V(2), SCD 211Y(3), SCD 230E(1), SCD 235Z(1), SCD 310D(28), SCD 373N(15), SCD 374J(8); SST 47C(3), SST 47D(3); LIZ 25M(1), LIZ 32Z(1); MB 40G(1), MB 54Y(1), MB 57A(4), MB 73N(4); KNY 166K; BRE 144C(1); L 476; X 22D; Y 12H; E 231; ZZ 30; T 13K; KN 2E; SS 55A; 33°S/27°E/120 m, 33°S/28°E/78 m (K. H. Barnard 1916); Port Elizabeth, East London (K. H. Barnard 1940).

Distribution: Mediterranean, Atlantic, Indian Ocean.

Lysianassa variegata (Stimpson, 1855)

Lysianassa variegata: Stebbing, 1888: 682, pl. 23.

Records: SCD 10U(2), SCD 148L(3), SCD 179M(1), SCD 181Y(1), SCD 189D(1), SCD 204T(1), SCD 262L(1), SCD 312S(2), SCD 338D(20), SCD 370M(14), SCD 376M(8), SCD 388E(1); SST 16W(1), SST 29N(1); LLL 6F; 33°S/26°E/18–29 m (Stebbing 1910a).

Distribution: Africa south of the equator.

Orchomene plicata (Schellenberg, 1925)

Orchomenopsis chilensis Schellenberg 1925: 119, fig. 3. K. H. Barnard 1925: 330.

Orchomenella plicata: K. H. Barnard, 1940: 440.

Records: SCD 20K(A), SCD 24G(3), SCD 287A(88); SST 65J(8); MB 28E(2), MB 61T(1), MB 73P(3); KNY 57C; Plettenberg Bay (K. H. Barnard 1940—as *Microlysias xenoceras*).

Distribution: Cosmopolitan.

Phoxostoma algoense K. H. Barnard, 1925

Phoxostoma algoense K. H. Barnard, 1925: 323, pl. 34, fig. 2.

Records: Algoa Bay, 65 m (K. H. Barnard 1925).

Diagnosis: Eyes large, meeting on top of head; body lacking carinae but with scattered setules; mouthparts forming a conical bundle; mandible slender, molar obsolete, palp attached proximal to molar; palp of maxilliped exceeding outer plate, article 4 small; gnathopod 1 simple, article 6 longer than 5; gnathopod 2 minutely chelate; third pleonal epimeron quadrate, telson deeply insinuate.

Distribution: Endemic to South Africa.

Socarnopsis crenulata Chevreux, 1910

Socarnopsis crenulata: K. H. Barnard, 1916: 124. Chevreux & Fage, 1925: 49, figs 31, 32.

Records: SCD 81E; SST 17Z(1), SST 29P(8), SST 32K(4), SST 34M(2), SST 45H(1); 33°S/27°E/120 m (K. H. Barnard 1916).

Diagnosis: Eyes large; upper lip and epistome together produced forwards into a lobe; mandibular molar ridged, palp attached proximal to molar, its second article very elongate; gnathopod 1 simple; dactyl of gnathopod 2 minute; gills plaited on both sides; outer ramus of uropod 3 with a minute second article; telson 80% cleft.

Distribution: Mediterranean, Atlantic, South Africa.

Stomacontion prionoplax Monod, 1937

Fig. 15

Stomacontion prionoplax Monod, 1937: 6, figs. 1-6.

Records: SCD 179N(1), SCD 244T(1).

Diagnosis: Coxa 1 rectangular, projecting over the side of the head and partly obscuring the eye; gnathopod 1 simple, article 5 as wide as long, dactyl powerful; articles 2 and 3 of pereopod 5 strongly lobed anteriorly; pleon segment 4 bearing a triangular dorsal carina; uropod 3 lacking rami or rami vestigial.

Distribution: This is the first record of this species from southern Africa. It was previously known only from the Suez Canal.

Remarks: The present material so closely resembles Monod's that I have no hesitation in equating the two. Of particular note is the identical structure of the mouthparts, particularly the unusual outer plate of the maxilliped, and of pereopod 5. The specimen figured here is much larger (5 mm) than Monod's and has smaller eyes. My other specimen, however, is of comparable size to Monod's and has similar sized eyes. The only significant feature distinguishing the South African form is the absence of the obscure vestigial ramus of uropod 3 described by Monod. The apparent variability of this feature, in addition to other intergrading features, renders the maintenance of any distinction between the genera *Stomacontion* and *Acontiosoma* superfluous, at least as they are defined at present, and the two genera should be united.

Trischizostoma remipes Stebbing, 1908

Trischizostoma remipes Stebbing, 1908a: 61, pl. 34. K. H. Barnard, 1925: 321.

Records: SCD 159P(10); SST 47A(2); 33°S/28°E/86 m, 34°S/23°E/58 m (Stebbing 1908a); 'Cape Point to East London' (K. H. Barnard 1916).

Distribution: Endemic, Natal to False Bay.

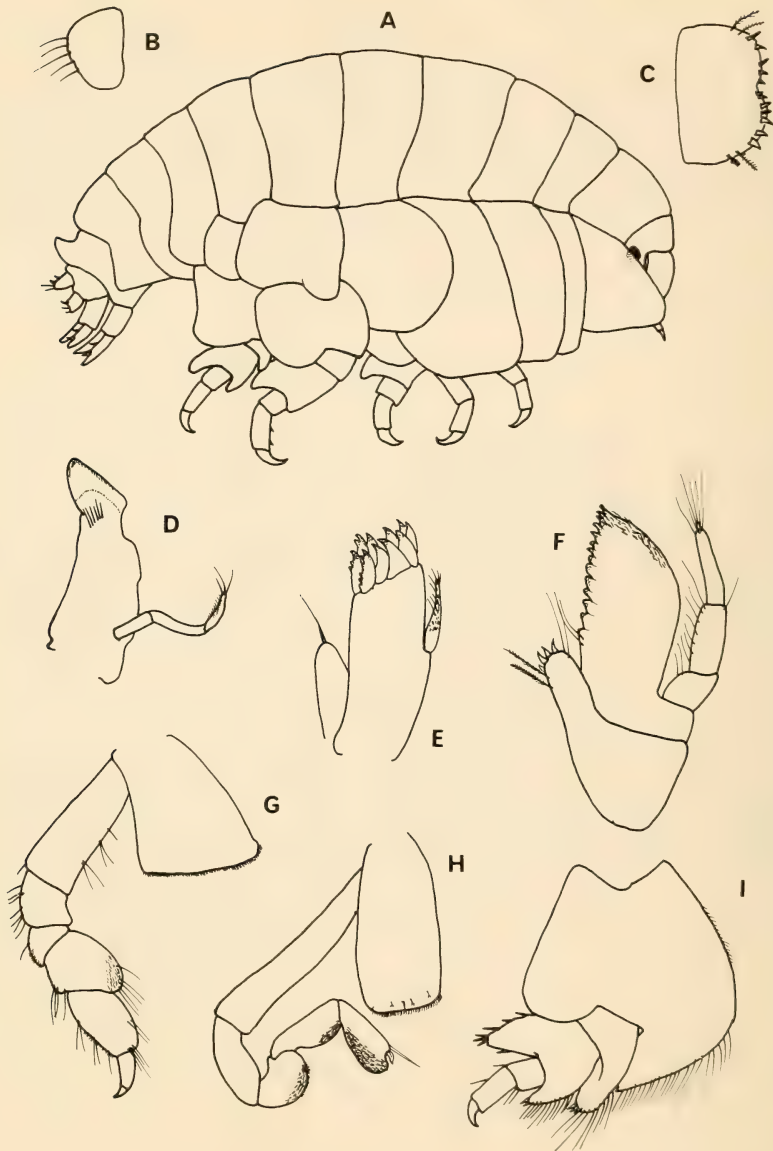


Fig. 15. *Stomacontion prionoplax* Monod, 1937
 Male, 5 mm: A—lateral aspect; B—uropod 3; C—telson; D—mandible;
 E—maxilla 1; F—maxilliped; G—gnathopod 1; H—gnathopod 2; I—pereiopod 5.

Trischizostoma serratum K. H. Barnard, 1925

Trischizostoma serratum K. H. Barnard, 1925: 320, pl. 34, fig. 1.

Records: SCD 366L(1).

Distribution: Endemic, Natal to False Bay.

Tryphosella africana K. H. Barnard, 1955

Tryphosella africana K. H. Barnard, 1955: 81.

Records: SCD 135E, SCD 198B(38), SCD 227T(1), SCD 236B(1), SCD 273F(3), SCD 338S(1), SCD 345W(9), SCD 348Z(11), SCD 349P(1), SCD 356U(2), SCD 376D(3), SCD 381U(1); SST 16X(1), SST 24S(2), SST 34L(1), SST 45G(2), SST 65C(5).

Diagnosis: Lateral lobes of head moderately acute, eyes absent; article 4 of antenna 1 male broadly oval, width more than half length; article 6 of gnathopod 1 ovoid, palm oblique, equal to hind margin; third pleonal epimeron greatly produced postero-distally into an acute upturned tooth; pleon segment 4 with a rounded dorsal hump; telson tapering evenly, bearing two pairs of dorsal spines and a spine and seta at apex of each lobe.

Distribution: Endemic to South Africa.

Tryphosella normalis K. H. Barnard, 1955

Tryphosella normalis K. H. Barnard, 1955: 80, fig. 39.

Records: SCD 110X(4), SCD 173Z(2), SCD 192Z(7); SST 5C(1), SST 18Z(4), SST 24T(1), SST 32L(1), SST 34D(3), SST 52R(3), SST 54F(1), SST 60L(2), SST 74F(1), SST 78G(2).

Distribution: Endemic, Natal to South West Africa.

Uristes sulcus n. sp.

Fig. 16

Description of female (3 mm): Head dorsally shorter than first two pereon segments, lateral lobes subacute, extending half length of article 1 of antenna 1; eyes obscure, composed of about seven scattered ommatidia; article 1 of antenna 1 large, longer than 2 and 3 together, flagellum 6-articulate, the first segment much the largest, accessory flagellum 3-articulate; antenna 2 exceeding 1, flagellum 9-articulate; mandible (Fig. 16B) with smooth heavily chitinized incisor, spine row of three spines, molar large, oval, ridged, palp 3-articulate, attached level with distal margin of molar; maxilla 1 (Fig. 16C) with two plumose setae at apex of inner plate, nine strong serrate spines at tip of outer plate, palp bi-articulate, terminating in nine small spine-teeth; palp of maxilliped (Fig. 16D)

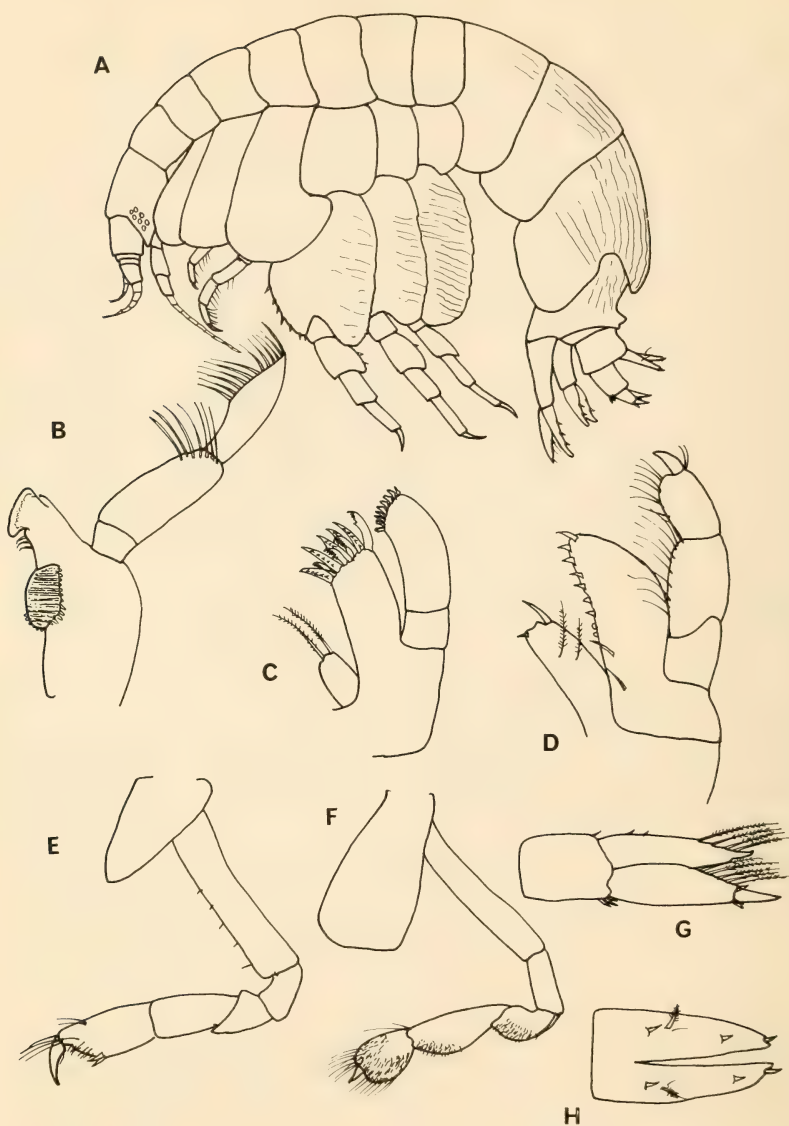


Fig. 16. *Uristes sulcus* n. sp.
 Female, 3 mm. A—lateral aspect; B—mandible; C—maxilla 1; D—maxilliped;
 E—gnathopod 1; F—gnathopod 2. Male, 4 mm: G—uropod 3; H—telson.

4-articulate, article 2 slightly longer than 1, article 4 small, outer plate with a row of nine spines along medial edge, inner plate bearing two plumose setae and two terminal spines.

Coxa 1 tapering evenly, about 80% length of coxa 2 which is rectangular and expanded somewhat distally; gnathopod 1 (Fig. 16E) subchelate, article 6 slightly longer than 5, palm oblique and subequal to hind margin, defined by two strong spines, dactyl without strong accessory tooth; gnathopod 2 (Fig. 16F) with setulose distal articles, 6 shorter than 5, palm transverse, dactyl small, partially concealed by setae; pereopods 1 and 2 slender; article 2 of pereopods 3–5 large, oval, bearing successively more obvious horizontal ridges.

Pleon segments 1–3 large, the integument bearing numerous longitudinal furrows and ridges, these being particularly obvious on the dorsal surface of pleon segment 3; pleonal epimera smoothly rounded; postero-dorsal section of pleon segment 3 produced as a hood-like lobe arching over proximal portion of pleon segment 4; pleon segment 4 with a small dorsal carina distally; outer ramus of uropod 1 slightly the longer, bearing three dorsal spines, inner ramus with two dorsal spines; outer ramus of uropod 2 with two dorsal spines, inner ramus not constructed, bearing a single medio-dorsal spine; peduncle of uropod 3 with a single dorsal spine and three ventral spines, rami naked, lanceolate, inner equal to article 1 of the outer; telson 80% cleft, a dorsal seta, two dorsal spines and a terminal spine to each lobe.

Male: The male of this species differs from the female by virtue of its longer second antennae, which reach half the length of the pereon, by the slightly larger carina on pleon segment 4 and by the setose third uropods (Fig. 16G).

Holotype: SAM A13224, male, 4 mm.

Type locality: SCD 230D, 34°04'S/23°26'E, 29 November 1960, depth 43 m, substrate yellow sand.

Relationships: J. L. Barnard (1962), in his revision of the genus *Uristes*, has drawn into it species previously assigned to some five other genera. The genus now contains species in which the condition of gnathopod 1 ranges from simple through to fully subchelate. *Uristes sulcus* n. sp. falls into that section, having an oblique, well-defined palm of gnathopod 1. It can be distinguished from others in that group by the presence of eyes and by the rounded pleonal epimeron, as well as by virtue of the unusual ridging on the pereopods and pleon from which its name has been derived.

Material: SCD 230D(2); SST 29L(1), SST 37X(2).

Uristes natalensis K. H. Barnard, 1916

Uristes natalensis K. H. Barnard, 1916: 126.

Records: 33°S/27°E/110 m (K. H. Barnard 1916).

Distribution: Endemic to south and east coasts of South Africa.

Family **Ochlesidae***Ochlesis lenticulosus* K. H. Barnard, 1940

Ochlesis lenticulosus K. H. Barnard, 1940: 447, fig. 23.

Records: SCD 244G(1); SST 11V(4).

Distribution: Endemic, Natal to False Bay.

Ochlesis levetzowi Schellenberg, 1953

Ochlesis levetzowi Schellenberg, 1953: 115, fig. 4. J. L. Barnard, 1969*b*: 372, fig. 134a.

Records: SCD 308G(5).

Distribution: Endemic, south coast of South Africa to South West Africa.

Family **Oedicerotidae***Periocolodes longimanus* (Bate & Westwood, 1868)

Periocolodes longimanus: Chevreux & Fage, 1925: 162, figs 163, 164.

Records: SCD 115E(1), SCD 122H(1), SCD 128T(1), SCD 135C(1), SCD 198V(6), SCD 202G(1), SCD 211W(3), SCD 225K(2), SCD 227X(1), SCD 244L(2), SCD 257K(5), SCD 267K(1), SCD 273J(3), SCD 276N(1), SCD 278H(7), SCD 282T(2), SCD 285M(2), SCD 329Z(1), SCD 332T(2), SCD 338F(18), SCD 339S(1), SCD 343X(1), SCD 345X(1), SCD 368R(1), SCD 376J(3), SCD 379P(3), SCD 381T(1), SCD 383S(1), SCD 391M(5); SST 24K(4), SST 29K(1), SST 32H(1), SST 34G(2), SST 40T(2), SST 45C(3), SST 52S(5), SST 54F(1), SST 56R(1), SST 60K(1), SST 61L(2), SST 63P(1), SST 65F(7), SST 67N(1), SST 73H(1), SST 76N(1), SST 78E(1), SST 81C(1).

Distribution: Mediterranean, Atlantic, Indian Ocean.

Westwoodilla manta n. sp.

Fig. 17

Description of male (6 mm): Head as long as first three pereon segments, rostrum almost half length of head (Fig. 17A), rod-like in shape, not deflexed, its apex smoothly rounded; eyes dorsally coalesced, situated at apex of rostrum; post-antennal angle of head rounded; antenna 1 slightly exceeding peduncle of antenna 2, flagellum 14-articulate; antenna 2 as long as pereon, flagellum 59-articulate; mandible (Fig. 17B) with 3-articulate palp, second article setose, moderately curved, article 3 subequal to 2, article 1 short, incisor of mandible not toothed but strongly chitinated, lacinia mobilis consisting of a small flattened plate, spine row of three spines, molar large, weakly ridged.

Coxa 1 marginally setose, distally expanded and produced forwards as a

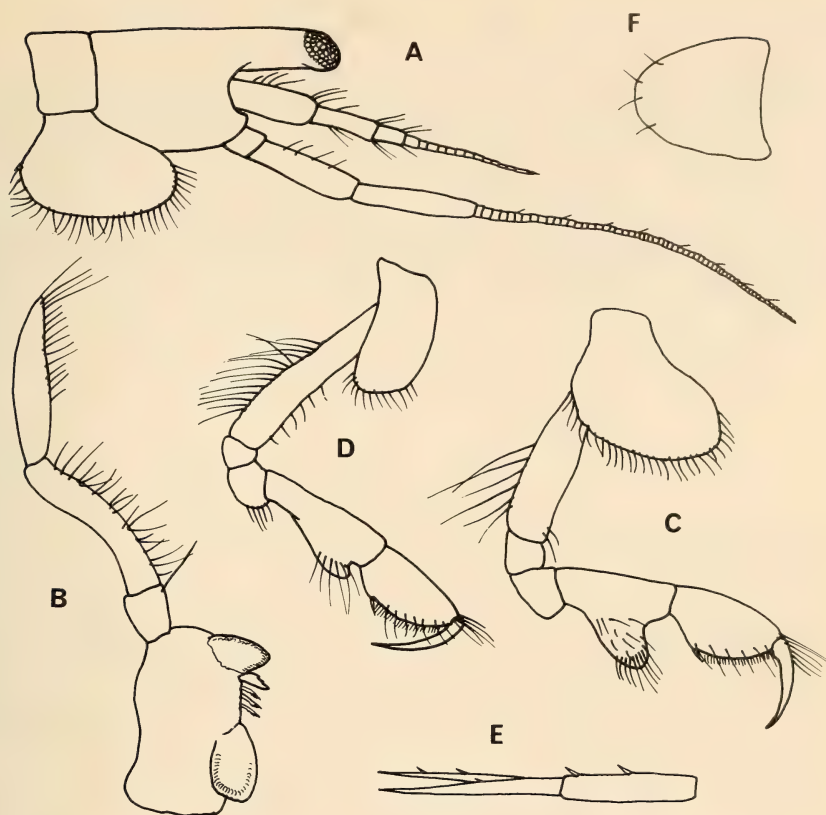


Fig. 17. *Westwoodilla manta* n. sp.
Male, 6 mm: A—head; B—mandible; C—gnathopod 1; D—gnathopod 2;
E—uropod 3; F—telson.

broad lobe; gnathopod 1 subchelate (Fig. 17C), article 5 moderately lobed, the lobe not protecting article 6 posteriorly, palm oblique, bearing alternating long and short setae, defined by a single small spine; coxa 2 rectangular; article 5 of gnathopod 2 (Fig. 17D) less strongly lobed than that of gnathopod 1, the lobe projecting at right-angles, not protecting article 6, palm oblique, setose, defined by a small spine; coxae 3 and 4 oval, 4 not excavate posteriorly, coxa 5 bilobed; pereiopods 1 and 2 slender, articles 4–6 strongly setose posteriorly, dactyl powerful, longer than article 6; pereiopods 3–5 successively larger, 5 very elongate.

Pleonal epimera smoothly rounded postero-distally; uropods 1–3 very slender, projecting equally, in each case outer ramus fractionally the shorter; telson (Fig. 17F) smoothly rounded, bearing four small setae distally.

Holotype: SAM A13223, male, 6 mm, unique.

Type locality: SCD 24W, 34°07'S/23°23'E, 26 May 1958, depth 46 m, substrate rock.

Relationships: The very elongate straight rostrum of this species is unusual. Most other members of the genus show a deflexed rostrum seldom extending to the tip of article 1 of antenna 1. Exceptions to this norm include *Westwoodilla acutifrons* Gurjanova, *W. longidactyla* Carausu and *W. rectirostris* Chevreux. However the rostrum of *W. acutifrons*, as the name suggests, terminates acutely and the eyes are medial rather than terminal. In *W. longidactyla* the eyes occupy the whole rostrum and the flagellum of antenna 1 does not exceed the length of articles 2 plus 3 of the peduncle. *W. rectirostris* bears the closest resemblance to *W. manta* n. sp. but differs from it by having longer antennae and the tip of the rostrum produced into an acute-tipped upturned process.

Family **Paramphithoidae**

Epimeria cornigera (Fabricius, 1779)

Epimeria cornigera: Chevreux & Fage, 1925: 191, figs 198–200.

Records: 33°S/28°E/550 m (K. H. Barnard 1916).

Diagnosis: Pereon segment 7 (and sometimes 6) and pleon segments 1–3 each bearing a pronounced dorsal carina flanked by a pair of subdorsal ridges; pleon segment 4 bearing a strong dorsal carina terminating in an acute tooth; coxae 1–5 all terminating acutely; third pleonal epimeron with an accessory tooth on posterior margin above the acute postero-distal corner.

Distribution: North Atlantic, Mediterranean, South Africa.

Family **Pardaliscidae**

Nicippe tumida Bruzelius, 1859

Nicippe tumida: J. L. Barnard, 1959b: 39–40, figs 1, 2.

Records: SCD 95K(1).

Diagnosis: Article 2 of antenna 1 shorter than article 1; gnathopods slightly subchelate, articles 5 and 6 stout, 5 with a large posterior lobe, shorter than 6, palm undefined; article 2 of pereopods 3–5 not inflated; pleon segment 4 bearing two contiguous small dorsal teeth; telson deeply cleft.

Distribution: Cosmopolitan.

Pardisynopia anacantha (K. H. Barnard, 1925)

Halice anacantha K. H. Barnard, 1925: 347, pl. 34, fig. 12.

Pardisynopia anacantha: J. L. Barnard, 1969b: 400.

Records: SCD 343Y(4); SST 17Y(2).

Diagnosis: Article 2 of antenna 1 shorter than article 1; flagellum of antenna 1

fully segmented, article 1 less than half length of peduncular article 1, accessory flagellum 2-articulate, basal article as long as articles 1–3 of primary flagellum; eyes absent; gnathopods simple; pereon and pleon without any dorsal teeth; third pleonal epimeron postero-distally quadrate; telson twice as long as broad, cleft nearly to base, lobes strongly dehiscent, their apices bifid.

Distribution: Endemic to South Africa.

Remarks: The above observations on the condition of antenna 1 confirm J. L. Barnard's provisional placing of this species in *Pardisynopia* (J. L. Barnard 1969b).

Family Phoxocephalidae

Mandibulophoxus stimpsoni (Stebbing, 1908)

Pontharpinia stimpsoni Stebbing, 1908a: 75, pl. 11.

Mandibulophoxus stimpsoni: J. L. Barnard, 1957: 436–438, figs 3, 4.

Records: SCD 83C(11), SCD 94X(1), SCD 104S(4), SCD 120A(1), SCD 122C(16), SCD 128R(9), SCD 138B(18), SCD 141N(1), SCD 141S(2), SCD 148G(15), SCD 151F(1), SCD 173S(2), SCD 188B(12), SCD 194V(3), SCD 198W(1), SCD 199G(3), SCD 202A(1), SCD 204P(3), SCD 211S(6), SCD 216N(1), SCD 222K(1), SCD 225G(4), SCD 228A(3), SCD 320A(6), SCD 232H(2), SCD 235V(1), SCD 262P(1), SCD 267H(4), SCD 273G(1), SCD 285K(11), SCD 286G(1), SCD 287B(1), SCD 288H(1), SCD 300T(1), SCD 310J(10), SCD 315W(8), SCD 321S(1), SCD 326J(1), SCD 329T(8), SCD 338B(15), SCD 343S(3), SCD 345T(9), SCD 348X(15), SCD 349L(8), SCD 350K(14), SCD 353K(2), SCD 356Q(2), SCD 370L(5), SCD 376E(9), SCD 381N(9), SCD 383R(3), SCD 384Q(4), SCD 391G(14), SCD 392V(4); SST 1C(1), SST 5D(3), SST 9A(3), SST 16C(2), SST 19C(4), SST 24G(10), SST 29A(52), SST 32A(7), SST 34C(17), SST 52Q(2), SST 54A(2), SST 56Q(16), SST 60H(13), SST 61K(4), SST 62L(3), SST 63N(1), SST 65A(7), SST 67L(4), SST 68P(8), SST 70N(7), SST 73E(6), SST 74C(5), SST 76L(3), SST 77B(18), SST 78F(2); MB 66U(4), MB 71G(3); 33°S/28°E/86 m, 33°S/26°E/18–29 m (Stebbing 1910a).

Distribution: West and South Africa.

Paraphoxus oculatus Sars, 1891

Paraphoxus oculatus: J. L. Barnard, 1960: 240–243, pls 27, 28.

Records: SST 81D(2).

Diagnosis: Rostrum tapering evenly in front of the eyes, apically rounded; third pleonal epimeron not produced postero-distally, outer surface without a setal row; article 6 of gnathopods 1 and 2 widened; telson cleft almost to base.

Distribution: Circumboreal.

Platyischnopus herdmani Walker, 1904

Platyischnopus capensis K. H. Barnard, 1925: 338, pl. 34, figs 13, 14.

Platyischnopus herdmani: Rabindranath, 1971: 521, figs 1, 2.

Records: SCD 198J(2), SCD 211U(1), SCD 244D(3), SCD 338N(2), SCD 376H(1); SCD 381W(1); SST 29J(1), SST 45B(1), SST 56T(1), SST 59J(1), SST 77C(1).

Distribution: India, South Africa.

Remarks: The genus *Platyischnopus* has been moved from Haustoriidae to Phoxocephalidae as proposed by Bousfield (1970).

Family **Podoceridae***Laetmatophilus purus* Stebbing, 1888

Laetmatophilus purus Stebbing, 1888: 1198, pl. 132.

Records: SCD 95H(1), SCD 127P(2), SCD 198K(1), SCD 204S(2), SCD 211T(2), SCD 216B(1); SST 32J(1); Q 7K; 34°S/25°E/138 m (K. H. Barnard 1916).

Distribution: Endemic, Moçambique to South West Africa.

Podocerus africanus K. H. Barnard, 1916

Podocerus africanus K. H. Barnard, 1916: 278, pl. 28, figs 24, 25; 1937: 176, fig. 19.

Records: LIZ 40D(8); J 11D; L 503; SS 55N.

Distribution: Arabia, Natal to South West Africa.

Podocerus brasiliensis (Dana, 1853)

Podocerus brasiliensis: J. L. Barnard, 1971: 117, figs 58–60.

Records: L 484, L 485.

Distribution: Cosmopolitan in tropical and temperate seas.

Podocerus cristatus (Thompson, 1879)

Podocerus cristatus: J. L. Barnard, 1962: 67, fig. 31.

Records: SCD 95B(2), SCD 102F(3), SCD 122G(1), SCD 302R(2), SCD 308H(4), SCD 392W(2); KNY 166L.

Distribution: Cosmopolitan in tropical and warm temperate seas.

Podocerus hystrix Stebbing, 1910

Podocerus hystrix Stebbing, 1910b: 622, pl. 58.

Records: SST 11P(16).

Diagnosis: Head with very short triangular rostrum and a large forward-directed

medio-dorsal process; pereon segment 1 with two medio-dorsal carinae; remaining pereon segments and pleon segments 1 and 2 bearing successively larger backward-directed processes each flanked by a pair of smaller lateral processes; lateral margins of pereon segments produced over the coxae; coxa 1 acutely produced forwards, 2-4 acutely produced ventrally; palm of gnathopod 2 defined by two spines, that of male with a small tooth near finger hinge.

Distribution: This is the first record of this species from Africa. It was previously known only from Australia.

Podocerus inconspicuus (Stebbing, 1888)

Podocerus palinuri K. H. Barnard, 1916: 277, pl. 28, fig. 23.

Podocerus inconspicuus: Nagata, 1965: 322, fig. 43.

Records: SCD 24H(1), SCD 55J(1), SCD 135A(2), SCD 146C(2), SCD 172W(2), SCD 208J(1), SCD 249T(1), SCD 283G(2), SCD 302S(3), SCD 345V(5), SCD 353E(6), SCD 356R(1); SST 24H(1), SST 29H(2); MB 16E(2), MB 57C(1), MB 87E(3); SS 55M; 34°S/22°E/215 m, 34°S/23°E/84 m (K. H. Barnard 1916).

Distribution: Indo-Pacific, west coast of South Africa.

Podocerus multispinis K. H. Barnard, 1925

Podocerus multispinis K. H. Barnard, 1925: 367, pl. 34, fig. 18.

Records: SCD 208F(2), SCD 353D(1); 34°S/25°E/128 m (K. H. Barnard 1916).

Distribution: Endemic, Natal to Saldanha Bay.

Family **Sebidae**

Seba saundersi Stebbing, 1875

Paravalettia chelata K. H. Barnard, 1916: 112, pl. 26, figs 2, 3.

Seba saundersii: K. H. Barnard, 1957: 7, fig. 4.

Records: 33°S/28°E/? (K. H. Barnard 1957).

Diagnosis: Eyes absent; gnathopod 1 subchelate in juvenile, becoming fully chelate in adult, article 6 with a notch on posterior margin bearing 4-5 plumose setae, dactyl closely fitting palm; gnathopod 2 smaller than 1, slender, chelate; article 4 of pereopods 3 and 4 acutely produced half length of article 5, that of pereopod 5 strongly expanded; telson entire, triangular, apically bluntly rounded.

Distribution: Cosmopolitan.

Family **Stegocephalidae**

Parandania boeckii (Stebbing, 1888)

Parandania boeckii: J. L. Barnard, 1961: 57, fig. 27.

Records: 33°S/28°E/900 m (K. H. Barnard 1916).

Diagnosis: Accessory flagellum of antenna 1 uni-articulate, almost as long as article 1 of primary flagellum, which exceeds half length of peduncle; mandibular incisor untoothed; palp of maxilla 1 uni-articulate; article 2 of pereopod 3 slender, that of pereopods 4 and 5 broad; telson oval, entire.

Distribution: Cosmopolitan, pelagic.

Stegocephaloides australis K. H. Barnard, 1916

Stegocephaloides australis K. H. Barnard, 1916: 129, pl. 28, fig. 29.

Records: SCD 181K(1); SST 1F(1), SST 9E(1), SST 11U(11), SST 19F(1), SST 24P(1).

Diagnosis: Head almost hidden under the tumid first pereon segment; eyes absent; coxae forming a continuous shield, 4 deeper than its pereon segment, the posterior and distal margins differentiated by a rounded angle; article 2 of pereopod 5 distally produced into an evenly rounded process reaching to apex of article 4; hind margin of article 2 of pereopod 5 feebly serrate; third pleonal epimeron postero-distally rounded.

Distribution: Endemic to South Africa.

Family **Stenothoidae**

Parametopa grandimana n. sp.

Fig. 18

Description of male (3 mm): Head slightly shorter than two pereon segments, eyes of moderate size, colourless; antenna 1 exceeding length of body, articles 1 and 2 subequal, each more than twice length of article 3, flagellum of 25 elongate articles, twice as long as peduncle, accessory flagellum absent; antenna 2 half as long as 1, flagellum 9-articulate; mandible (fig. 18B) with palp represented by a single seta, cutting edge strongly toothed, spine row of 10 spines, the first three pectinate, molar absent; palp of maxilla 1 (Fig. 18C) uni-articulate, tipped by seven spines, outer plate terminating in four strong serrate spines and two small simple ones, inner plate bearing single apical seta; outer plate of maxilla 2 (Fig. 18D) with four apical spines, inner plate bearing three setae; inner plates of maxilliped (Fig. 18E) small, each bearing a single spine, outer plate vestigial, palp 4-articulate.

Coxa 1 small, covered by coxa 2, which is produced anteriorly; coxa 3 rounded, bearing numerous chitinous (? stridulation) ridges along distal and posterior margins; coxa 4 very large, not posteriorly excavate; remaining coxae oval; gnathopod 1 small, subchelate, article 4 distally produced into a setose lobe, article 5 as long as 6, palm oblique, undefined; gnathopod 2 extremely large (Fig. 18A), antero-distal corners of articles 2 and 3 moderately lobed, article 5 cup-shaped, 6 tapering distally from defining angle; palm greatly exceed-

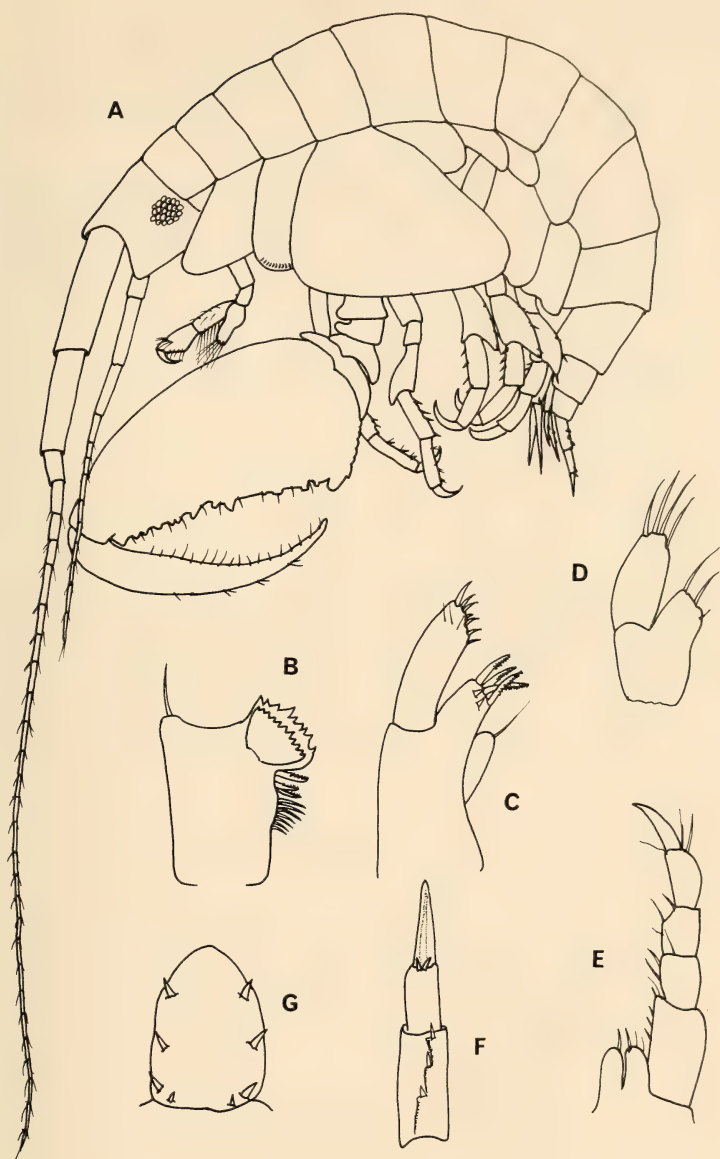


Fig. 18. *Parametopa grandimana* n. sp.
Male, 3 mm: A—lateral aspect; B—mandible; C—maxilla 1; D—maxilla 2;
E—maxilliped; F—uropod 3; G—telson.

ing hind margin, bearing about 12 small irregularly spaced teeth and scattered small setae, defined by a larger tooth, dactyl powerful, equal to palm, inner margin sparsely setose; pereopods 1–3 slender, article 2 linear, article 4 widening slightly distally; article 2 of pereopods 4 and 5 oval, article 4 expanded distally and postero-distally produced into an acute lobe bearing strong spines on both margins.

Pleonal epimera 1 and 2 rounded, 3 rounded-quadrate; peduncle of uropod 1 with two rows of 7–8 dorsal spines, rami equal, lanceolate, bearing one or two dorsal spines; uropod 2 half length of 1, outer ramus 70% length of inner, each with a single dorsal spine; peduncle of uropod 3 (Fig. 18F) with three dorsal spines, the single ramus consisting of two subequal articles, the first bearing two apical spines, the second dorsally pectinate; telson (Fig. 18G) entire, longer than broad, each lateral margin bearing one minute spine and three powerful ones.

Holotype: SAM A13216, male, 3 mm.

Type locality: SST 5F, 35°22'S/22°31'E, 20 June 1972, depth 200 m, substrate coarse khaki sand.

Relationships: Of the three existing species in this genus *P. grandimana* n. sp. can be distinguished from *P. alaskensis* (Holmes) and *P. kervillei* Chevreux by the shape and size of gnathopod 2. I have been unable to obtain a description of the third species—*P. sarniensis* (Norman)—but Chevreux & Fage, writing after Norman, state that all members of *Parametopa* known at that time have subequal antennae, a feature not consistent with the present species.

Material: SST 5F(10), SST 16K(6).

Proboloides rotunda (Stebbing, 1917)

Metopa rotundus Stebbing, 1917: 39, pl. 7A.

Records: SCD 122K(1), SCD 135L(2), SCD 159V(18), SCD 181Z(1), SCD 188F(2), SCD 198U(2), SCD 199E(2), SCD 204Y(1), SCD 211Z(1), SCD 222P(2), SCD 225N(1), SCD 345Y(3); 34°S/23°E/42 m (Stebbing 1917).

Distribution: Endemic to South Africa.

Stenothoe dolichopous K. H. Barnard, 1916

Stenothoe dolichopous K. H. Barnard, 1916: 153, pl. 26, figs 15–17.

Records: 32°S/28°E/176 m (K. H. Barnard 1916).

Diagnosis: Gnathopod 1 very elongate, articles 3 and 4 subequal, 5 equal to 2, 6 linear, shorter than 5, palm oblique, defined by two spines; articles 2 and 3 of gnathopod 2 antero-distally produced into rounded lobes, article 6 twice as long as broad, palm occupying whole posterior margin, a conical tooth at its centre, a second nearer the hinge and a large crenulate triangular process just

before the hinge; third pleonal epimeron with a minute postero-distal tooth; ramus of uropod 3 shorter than peduncle, second joint half length of first; telson oval, each lateral margin bearing three spines.

Distribution: The above record is the only one to date.

Stenothoe gallensis Walker, 1904

Stenothoe gallensis: J. L. Barnard, 1971: 120, figs 62, 63.

Records: KNY 166J, KNY 176E.

Distribution: Cosmopolitan.

Stenothoe valida Dana, 1853

Stenothoe valida: Sivaprakasam, 1967a: 373, fig. 2a-b. J. L. Barnard, 1970b: 250, fig. 165.

Records: SST 24N(1).

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Synopiidae**

Tiron australis Stebbing, 1908

Tiron australis Stebbing, 1908a: 79, pl. 38.

Records: SCD 110T(1), SCD 131Z(2), SCD 173U(1), SCD 370T(1), SCD 373M(5); SST 34P(1), SST 37A(1), SST 37Y(1); 33°S/28°E/86 m (Stebbing 1908a).

Distribution: Endemic to Indian Ocean coast of South Africa.

Superfamily **Talitroidea**

(Revised J. L. Barnard 1972b)

Family **Ceinidae**

Afrochiltonia capensis (K. H. Barnard, 1916)

Chiltonia capensis K. H. Barnard, 1916: 244, pl. 27, figs 38-40.

Afrochiltonia capensis: K. H. Barnard, 1955: 93.

Records: HAM 11C(C); HAV 5C(1), HAV 7L(P), HAV 18L(C); KNY 112C; STJ 24E(A), STJ 27F(C).

Distribution: Endemic, Natal to Saldanha Bay.

Family **Phliantidae**

Palinnotus natalensis K. H. Barnard, 1940

Palinnotus natalensis K. H. Barnard, 1940: 445, fig. 22.

Records: J 11E; Y 12J.

Distribution: India, east coast of South Africa.

Plioplateia triquetra K. H. Barnard, 1916

Plioplateia triquetra K. H. Barnard, 1916: 156, pl. 26, figs 18–24.

Records: SCD 302Y(2), SCD 310F(1); 33°S/27°E/91 m (K. H. Barnard 1916).

Diagnosis: Body as broad as deep, rostrum upturned, bearing a tooth on each side; antenna 1 half length of pereon; pereon segments 1–7 and pleon segments 1 and 2 each surmounted by a dorsal carina, that of pereon segment 1 deeply bifid; each pereonite also bearing a flat horizontal backwardly-directed lateral projection; maxilla 1 with palp; maxilliped bearing 4-articulate palp; gnathopods subchelate; uropod 3 represented by an oval lobe-like peduncle, rami absent.

Distribution: Endemic to south coast of South Africa.

Temnophlias capensis K. H. Barnard, 1916

Temnophlias capensis K. H. Barnard, 1916: 158, pl. 26, figs 25–35.

Records: S 54G; SS 55B; Still Bay (K. H. Barnard 1940).

Distribution: Endemic, Still Bay to South West Africa.

Family **Talitridae**Subfamily **Hyalinae***Allorchestes inquirendus* K. H. Barnard, 1940

Allorchestes inquirendus K. H. Barnard, 1940: 477, fig. 34b–c.

Records: MB 37L(1); Port Elizabeth (K. H. Barnard 1940).

Distribution: Endemic, Port Elizabeth to South West Africa.

Hyale grandicornis Kröyer, 1845

Hyale grandicornis: K. H. Barnard, 1955: 93, fig. 46. Hurley, 1957: 904–909, figs 1–23.

Records: KNY 166A, KNY 171C; J 11G; Q 7G; L 71; X 8A; K 8J; Y 12E; T 3G; KN 2H; SS 55F; Port Elizabeth, East London (K. H. Barnard 1916); Still Bay, Plettenberg Bay (K. H. Barnard 1940).

Distribution: Indo-Pacific, South Atlantic.

Hyale macrodactyla Stebbing, 1899

Hyale macrodactyla: Ledoyer, 1972: 273, fig. 77.

Records: H 9B.

Distribution: India, Madagascar, southern Africa.

Hyale maroubrae Stebbing, 1899

Hyale maroubrae: Hurley, 1957: 913, figs 51–71.

Records: KNY 166H(1), KNY 171D.

Diagnosis: Antenna 1 extending 30% along length of flagellum of antenna 2; coxae rectangular; palm of gnathopod 1 male transverse, defining angle ridged; article 2 of gnathopod 2 male not distally lobed, palm extending whole length of article 6, bearing two rows each of eight seta-tipped spines and defined by a shallow pocket into which the dactyl closes; article 6 of pereopods 1–5 postero-distally bearing a stout striated seta-tipped spine and a flattened fusiform striated spine.

Distribution: Indo-Pacific.

Hyale saldanha Chilton, 1912

Hyale saldanha Chilton, 1912: 509, pl. 2, figs 24–29.

Records: MB 40N(2); L 38Z; E 232; AR 1Q(8).

Distribution: Endemic, East London to South West Africa.

Subfamily **Talitrinae***Orchestia ancheidos* (K. H. Barnard, 1916)

Talorchestia ancheidos K. H. Barnard, 1916: 221, pl. 27, figs 35, 36.

Orchestia ancheidos: Ruffo, 1958: 43, figs 3, 4.

Records: BMR 21E(6); HAM 4B(A); HAV 13M(1); STJ 5B(C), STJ 29F; Keurbooms River, Plettenberg Bay (K. H. Barnard 1940).

Distribution: Madagascar, Moçambique, South Africa.

Orchestia rectipalma K. H. Barnard, 1940

Parorchestia tenuis (non Dana, 1853): K. H. Barnard, 1916: 226.

Parorchestia rectipalma K. H. Barnard, 1940: 473, fig. 32.

Records: HAM 11B(C), HAM 13C(C); HAV 7J(P), HAV 18E(C), HAV 20A(C); KNY 103A, KNY 175E, KNY 179A(C), KNY 181A(A), KNY 266C(5), KNY 272A(18), KNY 273B(60), KNY 274H(4), KNY 285A(C), KNY 286B(C), KNY 294A(47); BRE 13D(3), BRE 34K(4), BRE 55E(A), BRE 56F(1), BRE 57G(4), BRE 71N, BRE 123D(8); STJ 7Q, STJ 15N(C); Keurbooms River, Plettenberg Bay (K. H. Barnard 1940).

Distribution: Endemic, Natal to South West Africa, especially in estuaries.

Talorchestia australis K. H. Barnard, 1916

Talorchestia australis K. H. Barnard, 1916: 220, pl. 27, figs 33, 34; 1940, fig. 30.

Records: GBR 13D(1).

Distribution: Endemic, South West Africa to Moçambique.

Talorchestia capensis (Dana, 1853)

Talorchestia capensis: K. H. Barnard, 1916: 216; 1940: 470, fig. 28.

Records: KNY 43A, KNY 114A(C), KNY 166B, KNY 187A; BRE 5A(6), BRE 18A(10); STJ 5A(C); Keurbooms River, Plettenberg Bay (K. H. Barnard 1940).

Diagnosis: Male gnathopod 1 with article 5 not lobed distally, article 6 weakly lobed; palm of gnathopod 2 male oblique, spinose, medially with a semicircular incision which in adults occupies almost the entire palm, dactyl with a deep semicircular concavity near its base; pleonal epimera postero-distally rounded, their posterior margins distinctly crenulate.

Distribution: Mediterranean, Atlantic, south coast of South Africa.

Talorchestia inaequalipes K. H. Barnard, 1951

Talorchestia inaequalipes K. H. Barnard, 1951: 705, fig. 5a-b.

Records: KNY 113A(C), KNY 162B.

Diagnosis: Eyes dorsally separated by more than their diameter; coxa 2 not lobed posteriorly; articles 5 and 6 of gnathopod 1 male apically lobed; palm of gnathopod 2 male oblique, spinose, defined by a small pelucid lobe; article 2 of pereopod 5 weakly serrate posteriorly, articles 4 and 5 strongly expanded in male, oar-like; hind margins of pleonal epimera distinctly serrate, postero-distal corners quadrate.

Distribution: Endemic, Knysna to Saldanha Bay.

Suborder CAPRELLIDEA

Family Aeginellidae

Eupariambus fallax K. H. Barnard, 1957

Eupariambus fallax K. H. Barnard, 1957: 9, fig. 6.

Records: SST 29D(2), SST 45E(3).

Diagnosis: Antenna 1 without swimming setae; mandible with molar and 3-articulate palp; branchiae on segments 3 and 4; palm of gnathopod 2 with a large acute tooth at its centre; pereopods 1 and 2 absent, pereopod 3 reduced to a 2-articulate rudiment terminating in four or five setae; abdomen of male with one pair of rudimentary appendages.

Distribution: Endemic, Still Bay to west coast of South Africa.

Metaprotella macrodactylos Stebbing, 1910

Metaprotella macrodactylos Stebbing, 1910a: 469, pl. 48A.

Records: 33°S/26°E/18-29 m (Stebbing 1910a).

Distribution: Endemic, Natal to Port Elizabeth.

Orthoprotella mayeri K. H. Barnard, 1916

Orthoprotella mayeri K. H. Barnard, 1916: 284; 1925: 372.

Records: SCD 3U(2), SCD 60M(3), SCD 122J(2), SCD 160L(2), SCD 181G(11), SCD 204N(4), SCD 319Y(3); SST 11T(7), SST 18W(1), SST 24B(4), SST 37Q(2); 33°S/27°E/100 m, 34°S/22°E/86 m (K. H. Barnard 1916); Algoa Bay 184 m, 33°S/28°E/180 m, 34°S/25°E/133 m, 34°S/23°E/148 m (K. H. Barnard 1925).

Distribution: Indo-Pacific.

Pseudaeginella tristanensis (Stebbing, 1888)

Pseudaeginella tristanensis: Stephensen, 1949: 52, fig. 23.

Records: SCD 160K(1), SCD 181Z; L 455; East London (K. H. Barnard 1940).

Distribution: Tristan da Cunha, South Africa.

Family Caprellidae

Caprella cicur Mayer, 1903

Caprella cicur Mayer, 1903: 75, 97, pl. 4, figs 5-7, pl. 8, figs 3-5.

Records: SCD 202H(1), SCD 248L(1); J 11C; LLL 6C; Port Elizabeth 24-27 m, 33°S/26°E/18-29 m (Stebbing 1910a).

Distribution: Endemic, Natal to west coast of South Africa.

Caprella danilevskii Czerniavski, 1868

Caprella danilevskii: McCain, 1968: 22-25, figs 10, 11.

Records: J 11C; L 500; K 8H; E 236.

Distribution: Widespread, pantropical.

Caprella equilibra Say, 1818

Caprella equilibra: McCain, 1968: 25-30, figs 12, 13.

Records: SCD 179K(1), SCD 189T(6), SCD 192W(65), SCD 198G(1), SCD 244E(9), SCD 282U(4), SCD 283F(1), SCD 312N(35), SCD 329Y(1), SCD 338J(5), SCD 353L(1), SCD 379H(6); MB 37K(6), MB 54W(1); KNY 28B; Port Elizabeth (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Caprella natalensis Mayer, 1903

Caprella penantis (non Leach, 1814): Stebbing, 1910a: 465.

Caprella natalensis: Laubitz, 1972: 47, pl. 9, figs F, G, pl. 10, figs F-K.

Records: Port Elizabeth 24-27 m (Stebbing 1910a).

Distribution: Southern Africa, Tristan da Cunha, Pacific coast of North America.

Caprella penantis Leach, 1814

Caprella penantis: McCain, 1968: 33–40, figs 15, 16.

Records: MB 41J(1); D 272; L 335, L 455B; Y 12D.

Distribution: Cosmopolitan in tropical and temperate seas.

Caprella scaura Templeton, 1836

Caprella scaura: McCain, 1968: 40–44, figs 17, 18.

Records: MB 50U(5).

Distribution: Cosmopolitan.

Caprella triodous Stebbing, 1910

Caprella triodous Stebbing, 1910a: 467, pl. 48B.

Records: SCD 141W(1); 33°S/25°E/24–27 m (Stebbing 1910a).

Diagnosis: Head without rostrum; flagellum of antenna 1 12-articulate; antenna 2 shorter than peduncle of antenna 1; no spine between bases of second gnathopods; article 6 of gnathopod 2 elongate, distally widening, palm divided into three very large teeth; pereopods 3 and 4 each with a pair of serrate-ended clasping spines.

Distribution: Endemic to south coast of South Africa.

Hemiaegina minuta Mayer, 1890

Hemiaegina minuta: McCain, 1968: 61–64, figs 29, 30.

Records: SCD 179L(1); L 61A.

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Phtisicidae**

Caprellina longicollis (Nicolet, 1849)

Caprellina longicollis: McCain, 1969: 289, fig. 2.

Records: L 455A; 33°S/26°E/18–29 m, Port Elizabeth 24–27 m (Stebbing 1910a).

Distribution: Mediterranean, southern oceans.

Caprellina spiniger K. H. Barnard, 1916

Caprellina spiniger K. H. Barnard, 1916: 282, pl. 28, fig. 35.

Records: MB 50V(1).

Distribution: Endemic, Mossel Bay to Lüderitz.

Chaka leoni Griffiths, 1974

Chaka leoni Griffiths 1974b: 258, figs 7, 8.

Records: SCD 59E(1).

Distribution: Endemic to east and south coasts of South Africa.

Phtisica marina Slabber, 1769

Phtisica marina: K. H. Barnard, 1916: 283. McCain, 1968: 91-97, fig. 46.

Records: SCD 24P(1), SCD 135H(1), SCD 159T(4), SCD 160J(2), SCD 181H(7), SCD 188E(3), SCD 192X(10), SCD 216J(1), SCD 232G(4), SCD 345Z(2), SCD 347C(1); SST 11S(13), SST 29C(1); 34°S/23°E/84 m (K. H. Barnard 1916).

Distribution: Mediterranean, Black Sea, Atlantic, southern Africa.

SUMMARY

An account is presented of the known gammaridean and caprellid amphipod fauna of the Cape Province of South Africa east of 20°E (Cape Agulhas). The vast majority of the records has been derived from the extensive estuarine, littoral and benthic collections amassed by the University of Cape Town Ecological Survey, and with these have been incorporated all previous records from the literature. The collections total in excess of 12 000 individuals and from these 173 species have been recognized. Fourteen of the species and two genera are presented here as new to science. These are *Dikwa acrania* n. gen., n. sp. (Acanthonotozomatidae); *Ampelisca acris* n. sp.; *Colomastix keiskama* n. sp.; *Concholestes armatus* n. sp.; *Neomicrodeutopus nyala* n. sp.; *Cunicus profundus* n. gen., n. sp. (Haustoriidae); *Urothoe platypoda* n. sp.; *Parajassa chikoa* n. sp.; *Liljeborgia palmata* n. sp.; *Listriella sinuosa* n. sp.; *Lepidepecreum twalae* n. sp.; *Uristes sulcus* n. sp.; *Westwoodilla manta* n. sp. and *Parametopa grandimana* n. sp. In addition two species, *Stomacontion prionoplax* Monod and *Podocerus hystrix* Stebbing, are recorded for the first time from southern Africa. A fusion of the Lysianassid genera *Stomacontion* and *Acontiosoma* is advocated.

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C. L. Griffiths

THE AMPHIPODA OF SOUTHERN AFRICA

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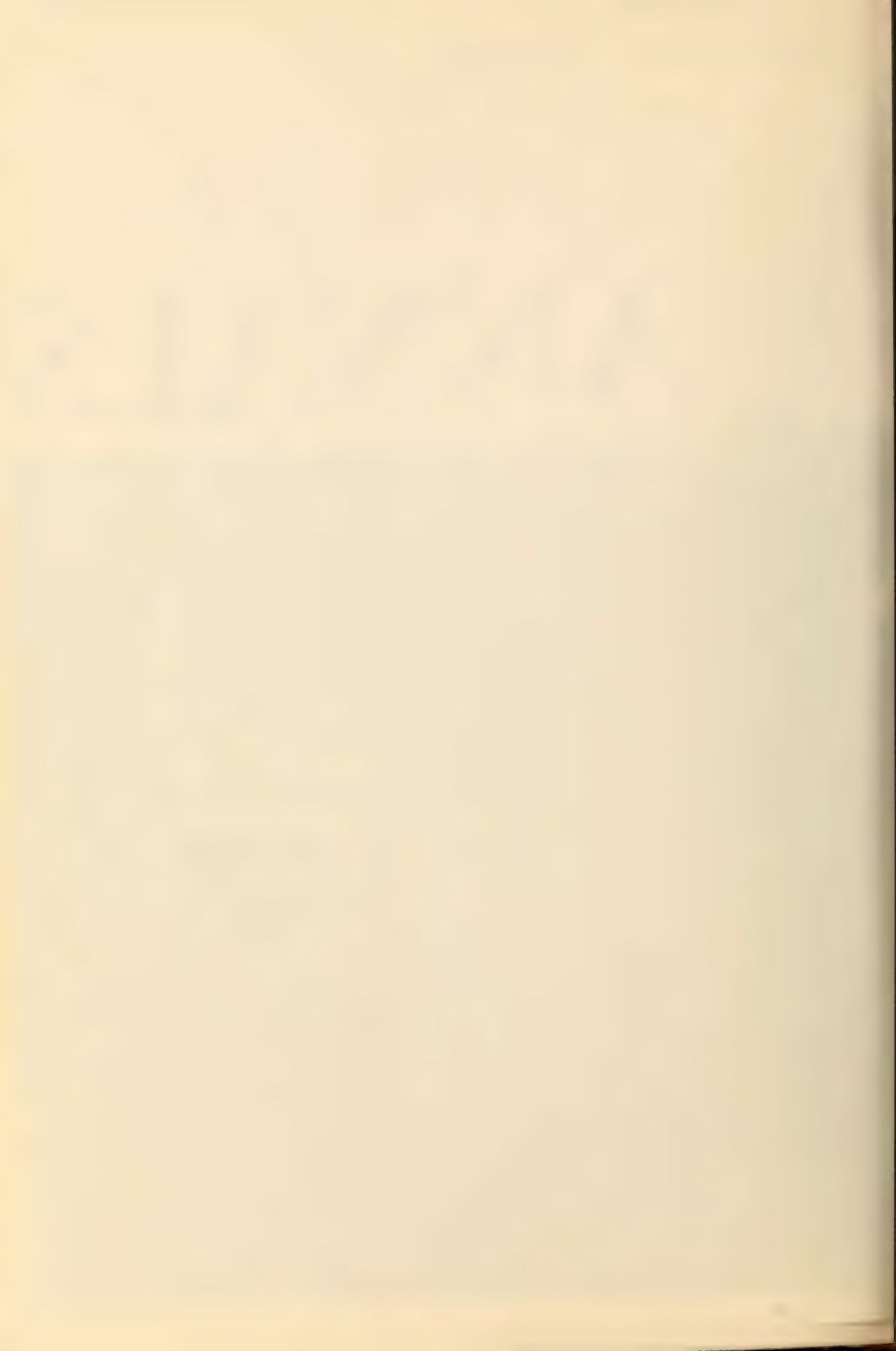
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By
S. FOURIE

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(With 33 figures)

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INTRODUCTION

When Owen introduced the term 'Cynodontia' in 1861, he made *Galesaurus*, which has a mammal-like dentition, the type of the new group which he called a 'family' of the order Anomodontia. Only in 1876 did he create the order Theriodontia to receive all forms with a carnivorous mammal-like dentition. *Lycosaurus*, *Nythosaurus* and *Scaloposaurus* were included in this order. The former, which was the type of the order, has simple, pointed teeth whereas the two other genera have laterally cuspidate postcanines. Obviously the Theriodontia were therefore meant by Owen to include more than his Cynodontia.

Because the crowns of the postcanines were not preserved in the *Galesaurus* specimen originally used by Owen (1861) as the type of his Cynodontia, Seeley (1895b: 59) proposed that the name Cynodontia be used for animals which resemble *Galesaurus* in skull structure and *Nythosaurus* in the structure of the postcanines, because it was possible to distinguish the Cynodontia from the Lycosauria (Theriodontia) '... by dental and other minor characters of the skull'. Seeley therefore designated *Cynognathus*, which he described in that year, as the type of the more narrowly defined Cynodontia. In 1903 Broom pointed out that the Theriodontia was not a natural order and proposed that it be broken down into Cynodontia and Therocephalia. Among these Cynodontia none is better known today than *Thrinaxodon*.

The first skull of *Thrinaxodon* was described by Owen in 1887, but he referred it to *Galesaurus planiceps*. In this identification he was followed by Seeley (1889) and Lydekker (1890). Only in 1895, on comparing the postcanine crown patterns of *Galesaurus planiceps* and *Nythosaurus larvatus* did Seeley

(1895a) realize that the skull belonged to a new genus and species for which he proposed the name *Thrinaxodon liorhinus*. Van Hoepen (1916), Gregory (1920) and Haughton (1920, 1924), when describing specimens now recognized as members of the genus *Thrinaxodon*, referred them to *Ictidopsis*, a name introduced by Broom in error in 1912. Since these two names refer to identical forms, the term *Thrinaxodon*, introduced by Seeley in 1894, has preference.

In 1932 Broom added the species *T. putterilli* to Seeley's original *T. liorhinus*. *Thrinaxodon* has become the best known of the Galesauridae and Cynodontia as a result of the studies of Broom published in several papers between 1910 and 1938, Watson (1920), Parrington (1933, 1935, 1936, 1939, 1946), Olson (1944), and Brink (1954, 1955b). More recently Estes (1961) elucidated the cranial structure of *Thrinaxodon* with emphasis on young individuals. Crompton (1963a) and Osborn & Crompton (1973) explained tooth replacement in *Thrinaxodon* and its significance in relation to mammalian evolution. Crompton & Jenkins (1968) demonstrated the importance of the dentition of *Thrinaxodon* in the evolution of molar teeth and the development of molar occlusion in the first mammals of the late Triassic. Hopson (1966), in a discussion of the origin of the mammalian middle ear, described the condition in *Thrinaxodon* and noted that the functional aspects of the cynodont middle ear are not understood well enough to say much about acuteness of hearing, but the largeness of the fenestra ovalis relative to the apparent size of the tympanum, which had an area of one-ninth or less of that of the former, would probably have made the sensitivity to sound much lower than in living reptiles.

Van Heerden (1972) has just completed a revision of some of the Galesauridae. He demonstrated the identity of *Thrinaxodon putterilli* with *Thrinaxodon liorhinus*. The type specimens of *Notictosaurus luckhoffii* and *N. gracilis*, declared identical with each other by Brink (1965), have now been shown to be identical with *T. liorhinus*. Van Heerden's investigations have greatly extended the territorial distribution of *Thrinaxodon* between Harrismith and vicinity in the north-eastern Orange Free State and Thaba N'chu more west and south, much further south to the vicinity of the Hendrik Verwoerd Dam near Bethulie, then on to the vicinity of Burgersdorp slightly more south-east and to Graaff-Reinet in the far south-west. Finally the value of the detailed description by Jenkins (1971) of the postcranial anatomy of *Thrinaxodon* and other African cynodonts should be mentioned in this brief survey of important contributions to our knowledge of *Thrinaxodon*.

In 1938 Broom had a skull sectioned at intervals of 4 to 5 mm. Considerable detail of internal structure and some of tooth replacement was obtained. The intervals between sections were, however, large and much detail was lost. Consequently accurate interpretations were difficult and several minor errors slipped in. Broom himself realized the inadequacy and suggested that a much larger series of sections and photographs be made in order '... to clear up all the characters of the prootic and opisthotic and to reveal the structure of the labyrinth'. Some of this additional information was obtained by Olson (1944)

when he sectioned a skull at intervals of 0,37 mm. He concentrated on the braincase, otic region and base of the skull.

Parrington's paper of 1946 added much new information, but it was felt that serial grinding at closer intervals than those taken in previous investigations might settle doubtful points, and reveal additional information especially on tooth replacement, the course of some of the nerves and blood vessels, the middle and inner ear, the relationships of the elements forming the braincase, the relationships of the postdentary bones, and the origins and insertions of jaw muscles and correlated skull structure. With this purpose in mind the study on which the present paper is based was started.

The skull of *Thrinaxodon liorhinus* Seeley selected for sectioning measured 67 mm from the tip of the snout to the posterior termination of the parietal crest. It was catalogued as number C354 of the National Museum, Bloemfontein, and was very well preserved, showing hardly any distortion. The snout was slightly damaged and the right postorbital arch was incomplete. Several detached pieces of bone lodged in the matrix were possibly derived from the broken regions. Serial grinding was done at intervals of 0,2 mm. Enlarged drawings were used for making graphic reconstructions and for building a wax plate model (5 ×, linear) of the skull. Crompton's (1955a) modified method based on the original technique described by Sollas (1914) and Olson (1944) was used. Photographs were taken of sections featuring important detail.

Before the completion of the original work on which this paper is based, the paper by Estes (1961) appeared which shed further light, especially on growth changes in the *Thrinaxodon* skull.

Through these studies the taxonomic position and external features of the skull and skeleton of *Thrinaxodon* have become well known. During the last five years it has become more and more evident that *Thrinaxodon* was an animal of crucial importance in the evolution of the first mammals.

In his discussion of the lower jaw of cynodonts and the evolutionary origin of the mammal-like adductor jaw musculature Barghusen (1968) showed that in *Thrinaxodon* a muscle mass with relationships approaching those of the mammalian masseter muscle had developed. The development of this musculature is intimately related to and can account for the relative posterior expansion of the ventral portion of the dentary ramus. This extra surface was included by the masseter muscle. Contrary to Crompton's (1963b) view, Barghusen shows that the adductor musculature did not migrate from the reflected lamina on to the ventral part of the masseteric fossa, but that the external adductor muscle (Crompton's deep masseter) on the dorsal lateral part of the dentary in procynosuchids migrated downwards (ventrally) and at the same time the entire length of the zygomatic arch was established as an area of muscular origin. The cynodont masseter is therefore a new differentiation not found in other therapsids.

The second change in cynodonts was the development of a pattern of insertion characteristic of the mammalian temporalis muscle. This was accomplished

through the posterodorsal expansion of the coronoid process of the dentary. As a result of these modifications cynodonts established an arrangement of adductor jaw musculature closely approaching that in living mammals. Crompton (1963*b*) had shown that in a stratigraphic series of cynodont lower jaws progressive osteological changes not found in any other group of reptiles took place. These changes were the progressive enlargement of the posterior part of of the dentary and concomitantly the reorientation in position and reduction in size of the accessory jawbones. Both Crompton and Barghusen relate the osteological changes in the lower jaw to the development of the mammalian type jaw musculature. Thus differentiation of jaw musculature in early cynodont evolution (procynosuchids to *Thrinaxodon*) is the key innovation that had profound significance for the origin of mammals.

In 1967 Hopson, in a discussion of mammal-like reptiles and the origin of mammals, concluded that early mammals could all be derived from small, probably insect-eating early Triassic cynodonts with skull and dental characters like those of *Thrinaxodon*. Some indication of the possible continued existence in the late Triassic of persistently small, dentally conservative cynodonts which were acquiring mammalian features in parallel with their larger more specialized relatives is a single poorly preserved skull of a very small cynodont with *Thrinaxodon*-like teeth from the Middle Triassic.

On the basis of the fact that the crown structure of one of the generations of postcanine teeth of *Thrinaxodon* is almost identical to that of *Eozostrodon*, except that the *Thrinaxodon* postcanines have a single root, and due to the overall primitive structure of the primitive cynodont skull, Crompton & Jenkins (1968) concluded that Rhaetic mammals (excluding ictidosaurids and haramyids) could be derived from primitive cynodonts. They point out that new material shows that it is possible to derive the cynodont petrosal and alisphenoid from that of a scaloposaurid, and that the eozostrodonid petrosal, as it is known at present, can be derived from that of an early cynodont of which the anterior margin is more complex than is shown in published accounts.

The view that mammals can be derived from persisting members of the cynodont family Galesauridae, of which *Thrinaxodon* is the most important known member, is reiterated by Hopson & Crompton (1969). They state that only cynodonts possess a large suite of features elsewhere found only in mammals. They believe that mammals had a monophyletic origin at the low taxonomic level of a family or even lower.

At present active research is being conducted on late cynodonts of East Africa and South America, in which information on the transitional stages between the early South African cynodonts and the first mammals is sought. In spite of all past and recent work, problems of functional anatomy and evolutionary transformation still remain. It is hoped that the results described in the present paper might, though obtained about ten years ago as part of the work for a doctoral thesis, still be able to contribute to the detailed comparison of structure in early and later cynodont and early mammalian skulls.

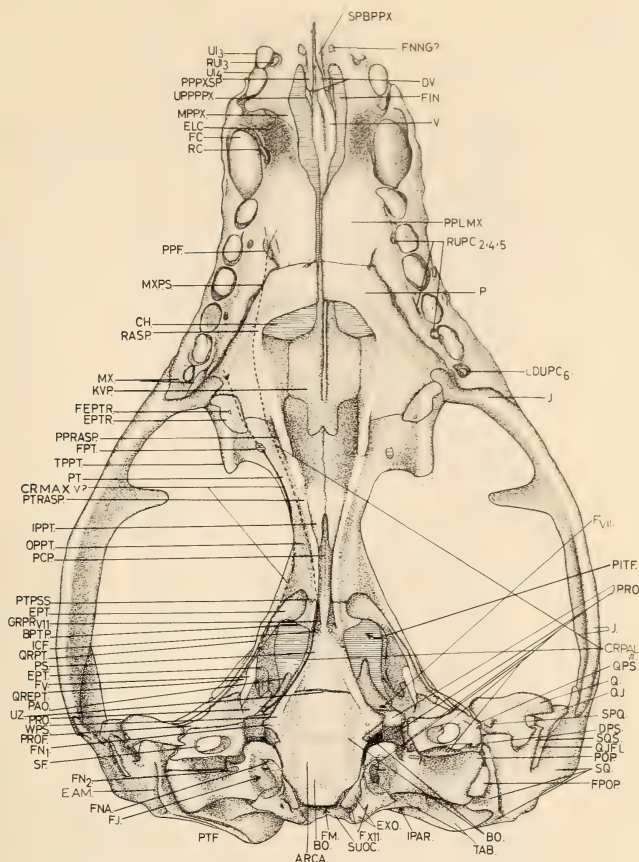


Fig. 1. Graphic reconstruction of ventral view of serially sectioned skull shown as a mirror image. $\times 1.5$.

DESCRIPTION OF MATERIAL

(a) SKULL (Figs 1, 2)

In this section only new details that have appeared from the present study will be mentioned.

Premaxillary (Figs 1, 3–6)

Behind the first incisor in each premaxillary is the small foramen (Figs 1, 33C, FNNG) of a vertical canal which may have had some connection with an organ of Jacobson or a nasal gland connected with the ability to detect odours. The canal appears to have a horizontal branch which opens on the anterior surface of the premaxillary immediately below the base of the internarial process. The vertical canal apparently opens on the floor

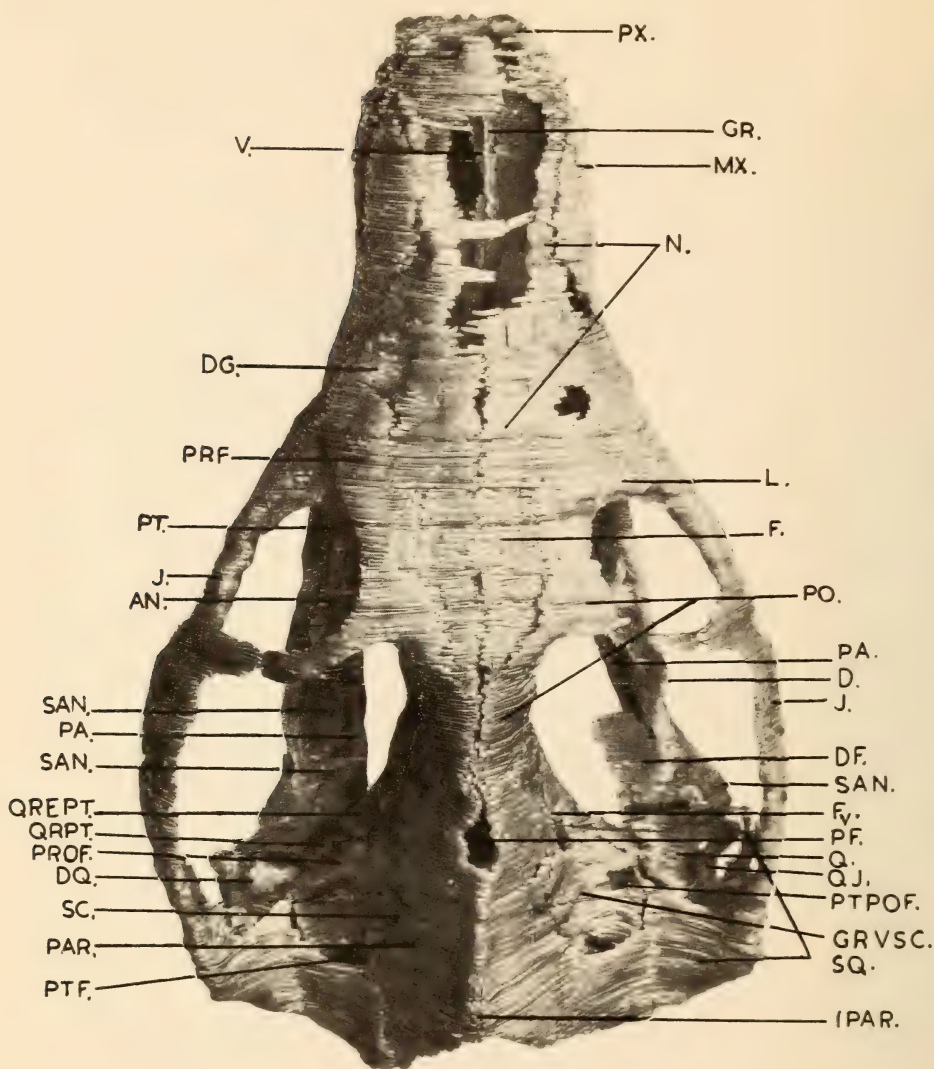


Fig. 2. Dorsal view of model of serially sectioned skull of *Thrinaxodon liorhinus* built on a linear magnification basis of $\times 5$. Roof of snout damaged. Photograph shows model reduced to $\times 2$ original size of skull.

of the nostril just behind the internarial process. It appears to be very similar to the canal described by Brink (1961*b*). Similar canals are present in the higher cynodonts as well as in primitive forms like the scaloposaurids.

In medial view, the palatal process of the premaxillary is bifid. The upper prong (Figs 1, 3A, 4B, 5, UPPPPX) is long and extends backward as far as the canines (Figs 1, 3A). The shorter lower prong (PPPXSP) in dorsal

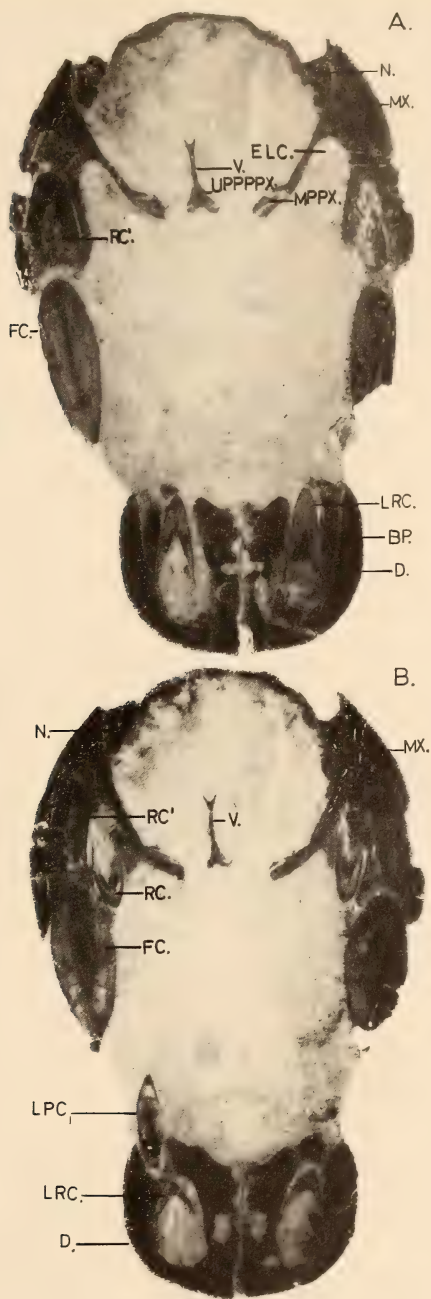


Fig. 3. A. Transverse section showing relationship of vomer, premaxillary and maxillary, and replaced upper canine; B. Transverse section showing replacing canine. Both $\times 3$.

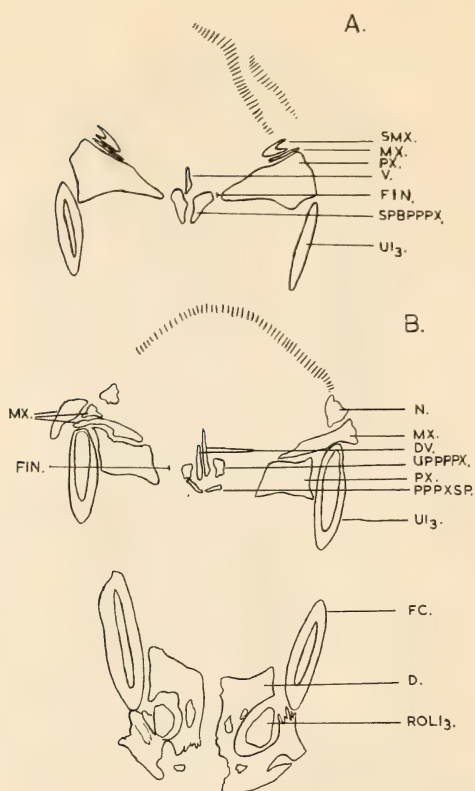


Fig. 4. Transverse sections through snout. A. Septomaxillary and palatal process of premaxillary. B. Double anterior end of vomer and palatal process of premaxillary. $\times 3$.

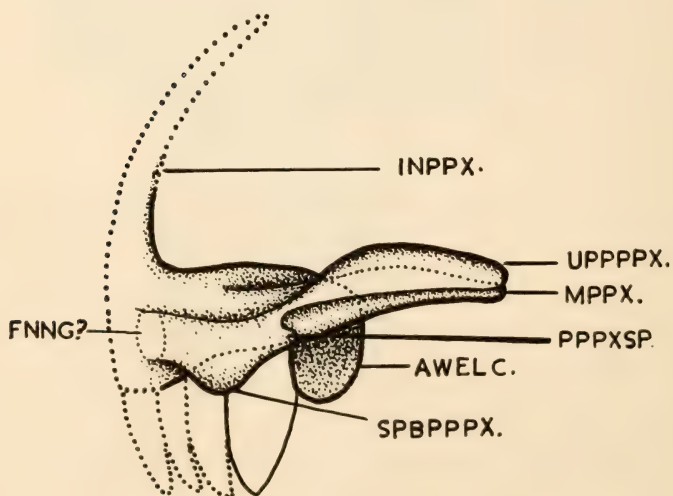


Fig. 5. Graphic reconstruction of medial view of premaxillary. $\times 5$.

view is partly hidden by the upper prong (Fig. 4B). In palatal view (Fig. 1), however, it largely obscures the upper (dorsal) prong. Ventrally at the base of the palatal process is a very small process (Figs 1, 4A, 5, SPBPPPX) situated on a low ridge along the medial ventral margin of the palatal process. A similar process is present in the cynognathids and *Diademodon* (Brink 1955a).

The lateral part of the premaxillary (i.e. palatal process excluded) forms the anterior wall of the pit for the lower canine. The premaxillary extends backwards medially alongside the ventral edge of the pit. This extension of the premaxillary (MPPX), referred to as the maxillary process of the premaxillary, is held in a groove along that part of the maxillary which forms the medial wall of this pit for the lower canine (Fig. 3A). A similar relationship is found in *Diademodon* and the cynognathids.

The anterior palatal foramen or foramen incisivum (Figs 1, 4A, B, FIN) is enclosed between the maxillary and palatal processes of the premaxillary. The ventral surface of the anterior part of the vomer (V) is clasped between the two palatal processes of the premaxillaries (Figs 1, 4A, B).

Maxillary (Figs 1–14A)

Most of the secondary palate is formed by the maxillary. The posterior palatal foramen (Figs 1, 9A, PPF) is about 2 mm long. It is situated on the suture between the maxillary and the palatine, but is largely formed by the maxillary. On the side wall of the snout the dorsal region of the maxillary (MX) lies lateral to the nasal (Figs 2, 3, 6B) and its posterior region overlaps the lacrimal (Figs 2, 6B, 9B, L).

It is interesting to note that many foramina (see e.g. Figs 8A, B, RHC), both large and small, perforate the anterior regions of the dentary, premaxillary and maxillary. The canals from these foramina join a single large canal in each side wall of the snout and in each ramus of the lower jaw. This fact lends support to the suggestion originally made by Watson (1931) when discussing the maxillary of the bauriamorph *Erciolacerta parva*. He stated (p. 1168): 'This surface is perforated by many foramina. . . . These foramina must have transmitted the blood-vessels and nerves to the skin of the face, their size suggesting that the nerves were exceptionally big, a condition only to be explained by the existence of a series of important tactile sense-organs grouped around the end of the muzzle, that is of what in a mammal would be a rhinarium.' However, Estes (1961) has shown that the vascularization of the *Thrinaxodon* snout does not necessarily indicate a rhinarium, since Van Valen (1960) has described similar vascularization in living reptiles such as *Tupinambis*. Estes claimed that the numerous foramina actually preclude the presence of a movable muscular cheek and lip.

Unfortunately, preservation of the anterior part of the maxillary is not perfect. There appears to be little doubt, however, that a big foramen is situated on the anterior part of the maxillary which forms the wall of the pit for the lower canine. (Estes (1961, pl. 2, fig. 1) actually shows a large foramen in this position.)

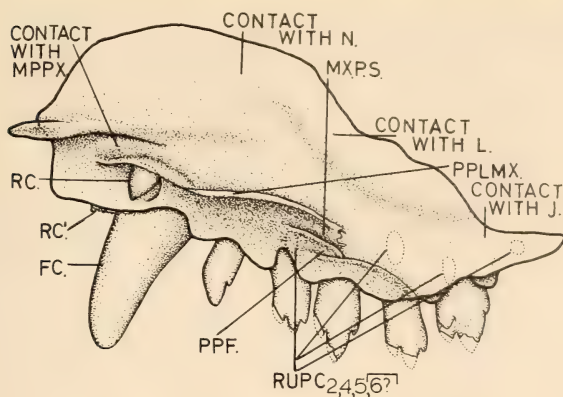


Fig. 7. Graphic reconstruction of maxillary in medial view.
× 2,5.

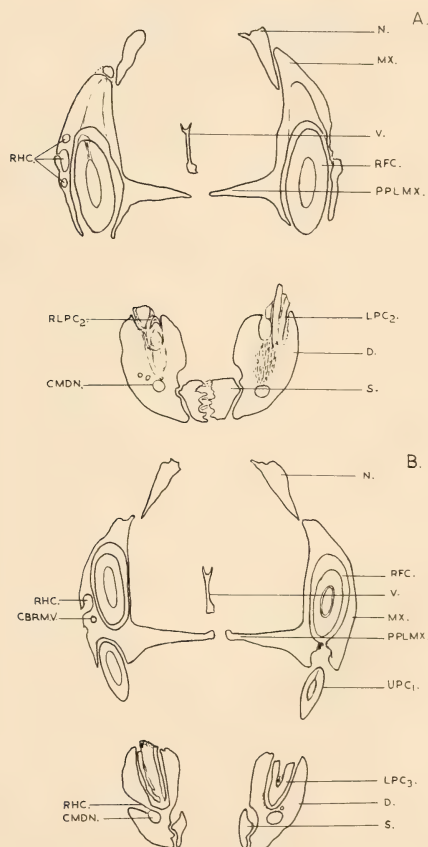


Fig. 8. Transverse sections through snout and lower jaw showing root of functional upper canine, foramina and canals in maxillary and dentary. Note splenial part of lower jaw symphysis in A. × 2,25.

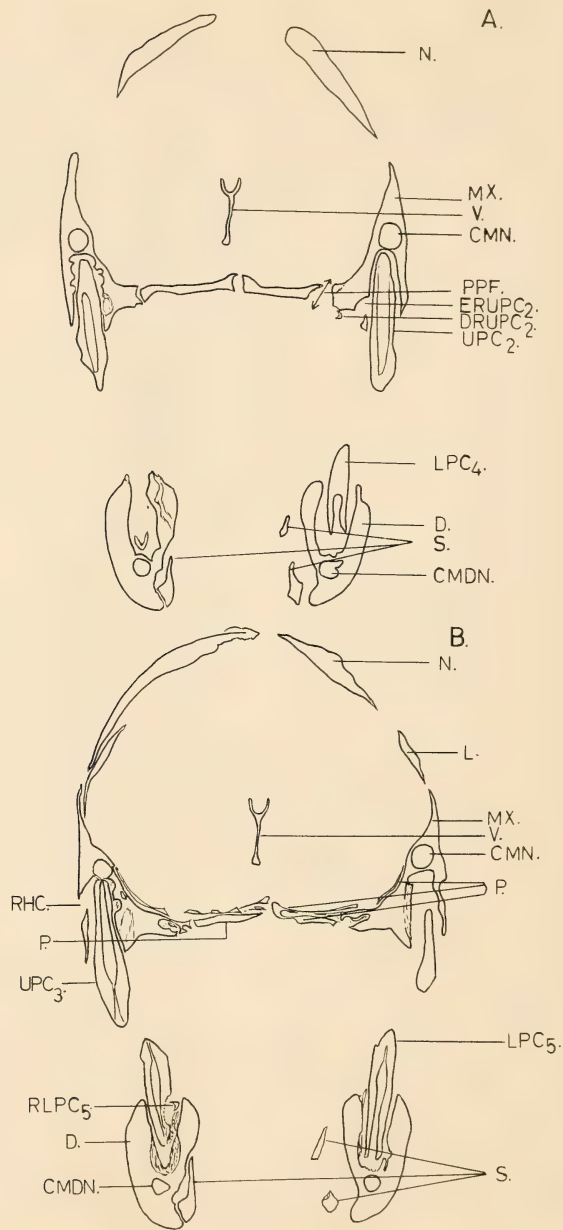


Fig. 9. Transverse sections through snout. A. Posterior palatal foramen; B. Maxillary-palatine suture in this region. $\times 2,5$.

outer surface of the maxillary. These canals join the maxillary canal which runs backwards in the bone. A small canal joins the base of the first postcanine alveolus with the maxillary canal running above it (Fig. 10). Further back the maxillary canal makes direct contact with the bases of the second and third postcanine alveoli. Several more little canals penetrate the maxillary walls of the postcanine alveoli and open into the alveoli. From here the nerves and/or blood-vessels in the canals may have been joined to the nerve and blood-vessels in the maxillary canal. After entering into the base of the third alveolus the main

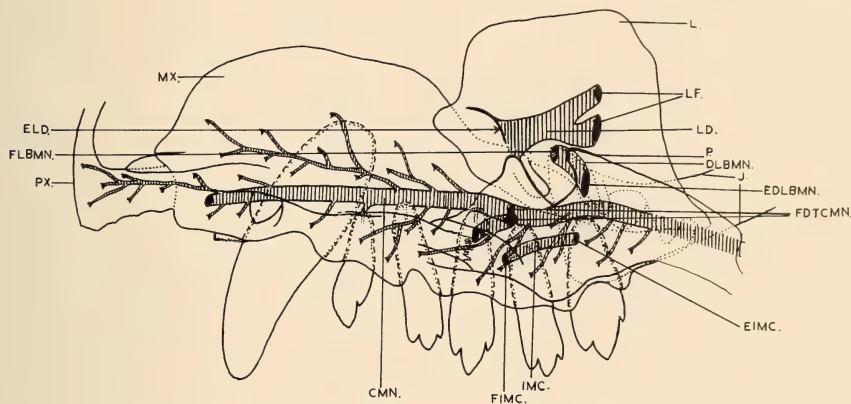


Fig. 10. Graphic reconstruction of canal system in wall of snout. $\times 2.5$.

maxillary canal is joined by a second one, the external opening of which is in the alveolar wall of the third postcanine (Figs 10, 13B, (F)DTCMN). These two canals enter (Fig. 13B₃, FDTCMN) into the 'maxillary antrum' (Fig. 13B₃, MAN) above the fourth postcanine alveolus and at a level just behind the transverse part of the maxillary-palatine suture. The foramen for this second branch of the ramus maxillaris of the trigeminal is also shown by Estes (1961, pl. 2, fig. 1). Kühne (1956, figs 4a, 5a) found that in *Oligokyphus* the ramus maxillaris also splits into two branches.

The maxillary antrum is formed in mammals by the maxillary only. In *Thrinaxodon* the posterior part of the maxillary has a considerable overlap with the lower part of the lacrimal laterally (see Figs 6, 10, MX, L) to form the outer wall of a cavity (Figs 11A, 13B₃, MAN). The floor of this cavity is formed by the maxillary, and its medial wall is formed by a dorso-laterally extending lamina of the palatine (Figs 12, 13B₃, P). This palatine lamina overlaps the lower part of the lacrimal, which forms the roof of the cavity, medially. The 'maxillary antrum' thus formed extends back as far as the sixth postcanine. Its medial wall is not complete, being interrupted behind the palatine lamina where the antrum is only a high, but shallow recess below the anterior part of the lacrimal. The palatine and lacrimal are then reunited in a serrated suture to form a solid

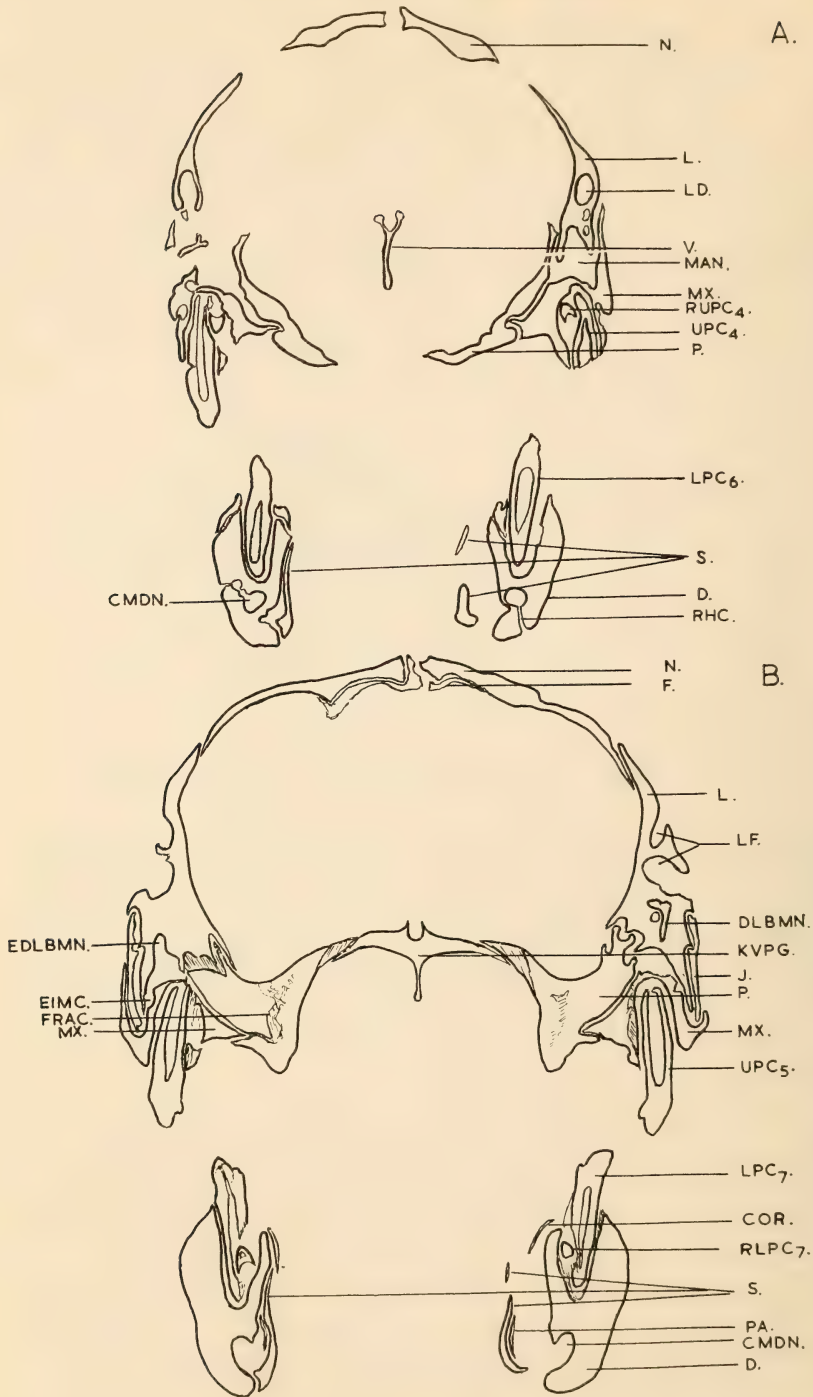


Fig. 11. Transverse sections through snout in the region of: A. Choanae and maxillary antrum; B. Roof of nasopharyngeal passage and lacrimal foramina. Note: relationships of maxillary, palatine, lacrimal and jugal; shape of vomer; structure of lower jaw especially as far as position of mandibular canal is concerned. $\times 3$.

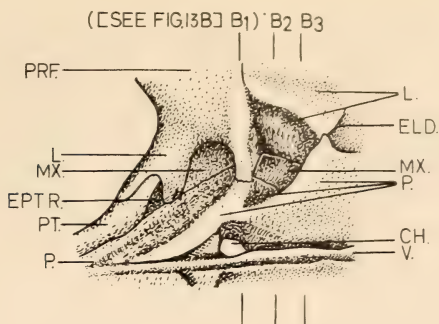


Fig. 12. Medial view of wall of snout of enlarged wax reconstruction of serially sectioned skull to show shapes and relationships of bones along the various parts of the maxillary antrum. $\times 2,5$.

bridge of bone lateral to which the 'maxillary antrum' continues (Figs 11A, 12). At this level the jugal (Fig. 11B, J) takes part in the lateral wall of the antrum. It is held between the lacrimal medially and a lamina of the maxillary laterally. The anterior palatine-lacrimal contact is 1,2 mm and the posterior bridge 1,4 mm in length. Beyond this bridge the antrum continues as a low, but deep recess 2,6 mm long, between the lacrimal and the maxillary (Fig. 12). The recess becomes progressively lower and ends at the level of the posterior margin of the sixth upper postcanine.

In lateral view the foramen of a canal (Figs 10, 13B, IMC), which penetrates the maxillary for 3 mm, is present at the level of the anterior border of the fourth upper postcanine and the 'maxillary antrum'. This canal opens posteriorly into the 'maxillary antrum' at the level of the palatine-lacrimal bridge. Its actual opening (Figs 10, 11B, EIMC) is medially at the base of the lateral lamina of the maxillary and directly below the lateral lower margin of the lacrimal, both of which take part in the formation of the outer wall of the antrum. The significance of the canal described here is uncertain, but it may have been for a third branch of the maxillary ramus of the trigeminal nerve. The latter appears to have swung down from behind the 'maxillary antrum' on to the dorsal surface of the palatine. Here it might possibly have been joined by the ramus palatinus of the facial nerve (Fig. 16A, CRPAL_{vii}) which probably left the palate through the posterior palatal foramen (Figs 1, 16A, B, PPF). Both branches then apparently continued further backwards on the pterygoid. Their further course is discussed below (see Pterygoid, p. 357).

Lacrimal (Figs 2, 6, 10–14A)

The lacrimal forms the anterior wall of the orbit (Fig. 6B). It extends forward as far as the third upper postcanine and the transverse part of the maxillary-palatine suture on the secondary palate. In sections the lacrimal appears mainly

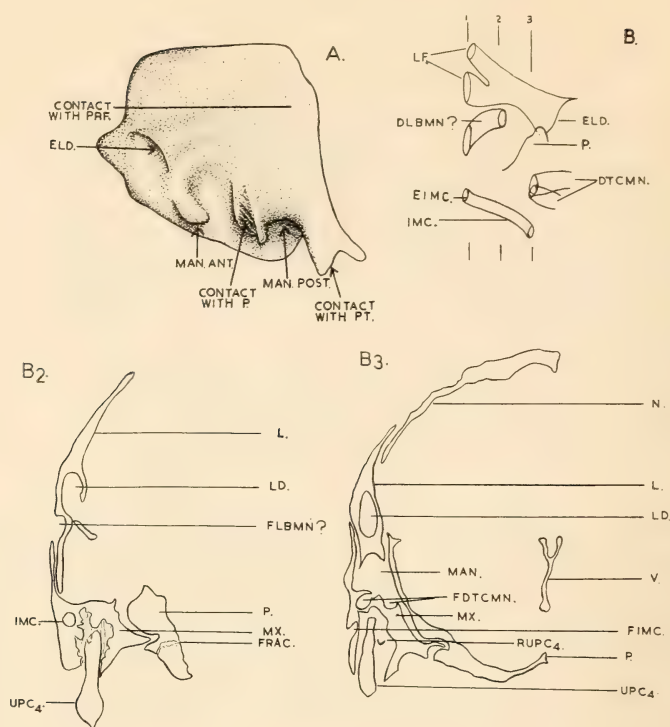


Fig. 13. A. Graphic reconstruction of medial view of lacrimal. B. Canals in wall of snout also shown in Fig. 10. Numbered levels coincide with those shown in Fig. 12. B₂ and B₃ are transverse sections from levels numbered 2 and 3 in B, or B₂ and B₃ in Fig. 12. $\times 2.5$.

as a thin sliver of bone with the exception of a thickened middle part which contains the lacrimal duct. In lateral view the lower part of the bone is overlapped by the posterior part of the maxillary, and the dorsal part of the lacrimal is just overlapped by the ventral margin of the posterior part of the nasal (Fig. 6A, MX, L, N). Unfortunately the preservation of this part of the snout is not as good as could be desired and the sections are difficult to interpret. The lacrimal also overlaps the anterior ventral part of the prefrontal (Fig. 6A, PRF). The anterior opening of the lacrimal duct (Figs 6A, 10, 12, 13A, B, ELD) is near the anterior end of the bone just above and in front of the anterior part of the wall of the 'maxillary antrum'. The maxillary forms a distinct ledge below the opening. In a posterior direction this ledge becomes more pronounced to form the floor of the 'maxillary antrum', but in front of the opening the ledge very gradually becomes indistinct.

Where the palatine and the lacrimal form the bridge which is part of the inner wall of the 'maxillary antrum' described above (see Maxillary), the lower

part of the lacrimal is wider than anywhere else when seen in section (see e.g. Fig. 11B, L). Between the fourth and fifth upper postcanines is the anterior foramen (Figs 10, 13B₂, FLBMN) (Estes (1961, pl. 2, fig 1) also shows this foramen) of a canal (Figs 10, 13B, DLBMN) which runs in the lacrimal just below the lacrimal duct. The lacrimal duct itself divides into a small upper and a larger lower duct only 1 mm behind the level of the foramen just mentioned (Figs 10, 13B) and opens (Figs 10, 11B, 13B, LF) into the orbit only 0.6 mm behind the division. The other canal turns sharply downward (Figs 10, 11B, 13B DLBMN) at this level and enters (Fig. 11B, EDLBMN) into the posterior part of the 'maxillary antrum', the inner wall of which is formed at this level by the palatine-lacrimal 'bridge'. This canal appears to be comparable with the one which Kühne (1956: 28, fig. 5) described in *Oligokyphus* as the canal for the lacrimal branch of the maxillary ramus of the trigeminal nerve.

It seems reasonable to assume, on the basis of the canals described above in the maxillary and lacrimal, that the ramus maxillaris of the trigeminal nerve was made up of the following branches (Fig. 10):

- (a) the main anterior branch made up of smaller branches from the tip of the snout, the incisors, the canine, the first two postcanines and the snout in their vicinity, joined by
- (b) a second branch from the side of the snout in the vicinity of the third postcanine. These two branches (a and b) entered the 'maxillary antrum', in the posterior part of which they were joined by
- (c) an independent branch of unknown significance, possibly a third branch of the ramus maxillaris, and
- (d) a lacrimal branch.

The compound maxillary ramus then left the 'maxillary antrum' and might have been joined a little further back by the ramus palatinus of the facial nerve.

The wide basal part of the lacrimal just in front of the narrower posterior end of the bone has a somewhat spongy structure which makes it difficult to reconstruct the course of a possible canal in this part of the bone from serial sections. There does, however, appear to be a canal which may then be compared with the vascular canal found by Kühne (1956: 28, fig. 5) in *Oligokyphus*.

Palatine (Figs 1, 6A, 9B, 11A-16B)

The maxillary is continued postero-laterally beyond the posterior palatal foramen, but it is overlapped on its medio-dorsal surface by the palatine (Figs 11A, 12, 13B₂, 13B₃, P, MX). This overlapping dorsal part of the palatine has a very thin upper rim of which the margin is expanded laterally and medially to form a distinct ridge. It is this thin upper end which forms the medial wall of the anterior part of the 'maxillary antrum' (Figs 12, 13B₃, P, MAN), the ridge being in contact with the medial surface of the lacrimal. The palatine and the maxillary are joined by a thin ledge which projects from the medial border of the maxillary into a groove along the lower lateral surface of the palatine (Figs 11,

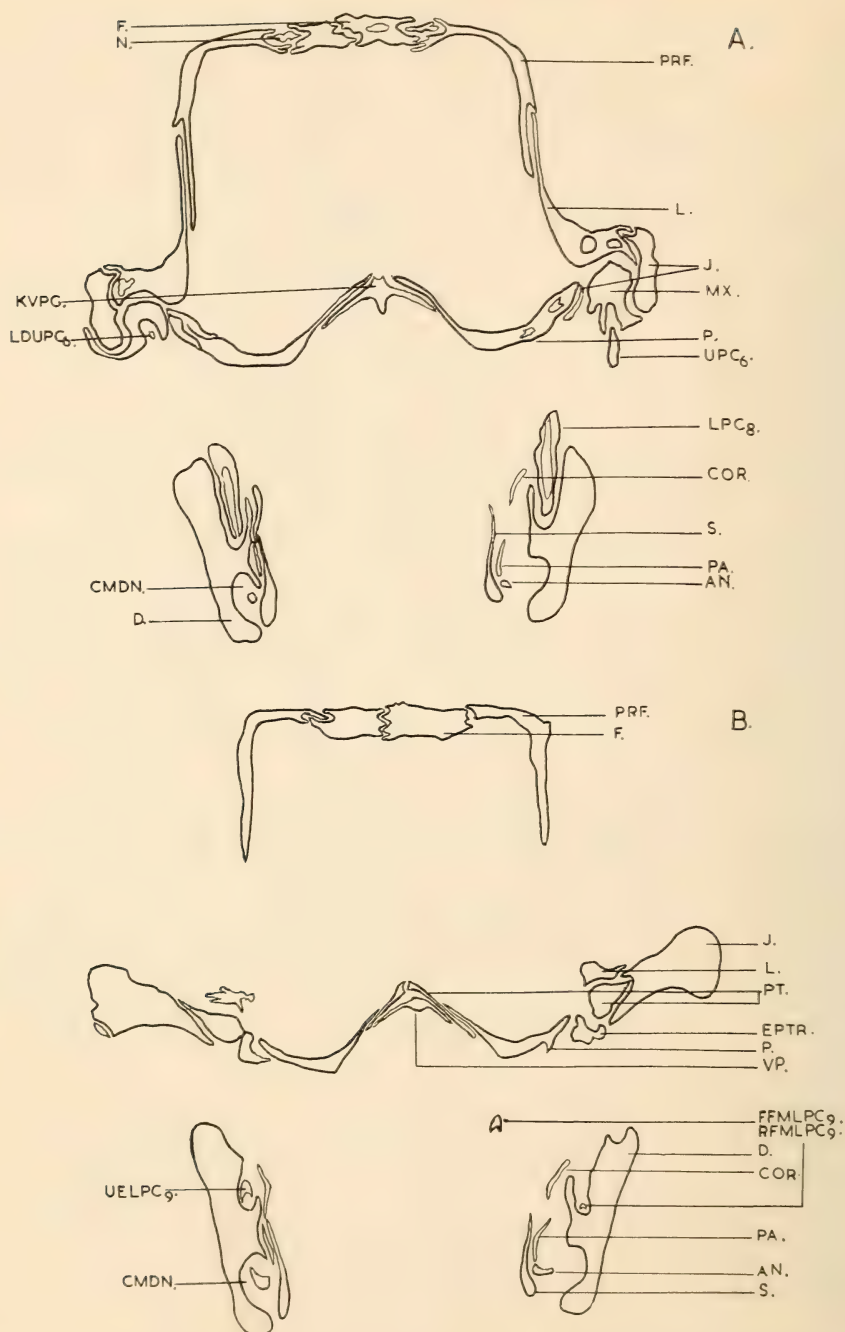


Fig. 14. Transverse sections through skull and lower jaw; A. At level in anterior part of orbit; B. Slightly further back. Note: anterior ends of pterygoids and ectopterygoids in B and of the angulars in A; posterior ends of nasals and maxillaries in A and of the lacrimals in B; extension laterally of jugals. $\times 2.5$.

13B₂, B₃) (a schindylesis or wedge-and-groove suture). The two bones lie close together at all their contact surfaces.

Ectopterygoid (Figs 1, 14A, 15A, 16A)

Parrington (1946) describes two foramina in this bone, but it seems to be a variable feature since the sectioned skull shows only one (Fig. 1, FEPTR). This single foramen is situated almost in the position of Parrington's anterior one, but it lies nearer the inner surface of the ridge.

Vomer (Figs 1, 3, 4, 6A, 8A–9B, 11A–12, 13B₃, 14A–15A)

The vomer has several features of interest. The posterior curved plate-like part forms the roof of the nasopharyngeal passage behind the secondary palate (Figs 1, 11B, 14A, B, (K)VP(G)). Antero-dorsally it is overlapped by the palatines (Figs 1, 4A, P) and postero-dorsally by the pterygoids (Figs 1, 14B, PT). The part comprising the thin median vertical plate extends forward into the lower half of the snout (Figs 1, 6A, 11A, V) to be clasped anteriorly by the upper prongs of the palatal processes of the premaxillaries (Figs 1, 3A, 4B, 6A, UPPPPX). Nowhere is the median vertical plate of the vomer in contact with the maxillaries. The front end of the vertical plate, which extends forward to a level with the fourth incisors, is bilaterally paired for a distance of 3.4 mm (Figs 1, 4B, 6A). A line of fusion can, however, be distinguished much further back. Anteriorly the lower end of each plate curls slightly outwards, but behind the line of fusion and as far back as the posterior border of the lower canine pit they curl pronouncedly (Figs 1, 3A, B). This condition is also found in higher cynodonts investigated by the present author and by Broili & Schröder (1934a). It need not cast doubt on the homology (proposed by Parrington & Westoll 1940) of this structure and the mammalian vomer which usually arises singly, since De Beer (1937: 434) gives examples of a paired origin of the vomer in mammals.

Together with the upper prongs of the palatal processes of the premaxillaries (UPPPPX) which also extend back to the level of the posterior margins of the lower canine pits, the vomer with its curling lower ends forms a rod in which the component parts support each other. This rod, of which the ventral surface is grooved (due to the curling vomer), divides the large foramen, situated ventrally between the premaxillaries, into a left and right foramen incisivum (Figs 1, 4A, B, FIN). The palatal plates of the maxillaries form the posterior border of each foramen. Above the palatal plates of the maxillaries, but not in contact with them, lies the vertical vomer plate of which the ventral margin is, in this region, thickened and rounded (Figs 1, 8A, B, V). The upper margin of this vomer plate has a distinct groove (Figs 3, 6A, GR). The groove extends back over the whole length of the vomer (Figs 3, 6A–11B, 14A), presumably over the pterygoids (where it may, however, be interrupted) and on to the rostrum of the parasphenoid (Figs 6A, 15C, 16A, 17, PCP). A similar condition is found in the cynognathids and in *Diademodon* (Brink 1955a). This groove probably supported

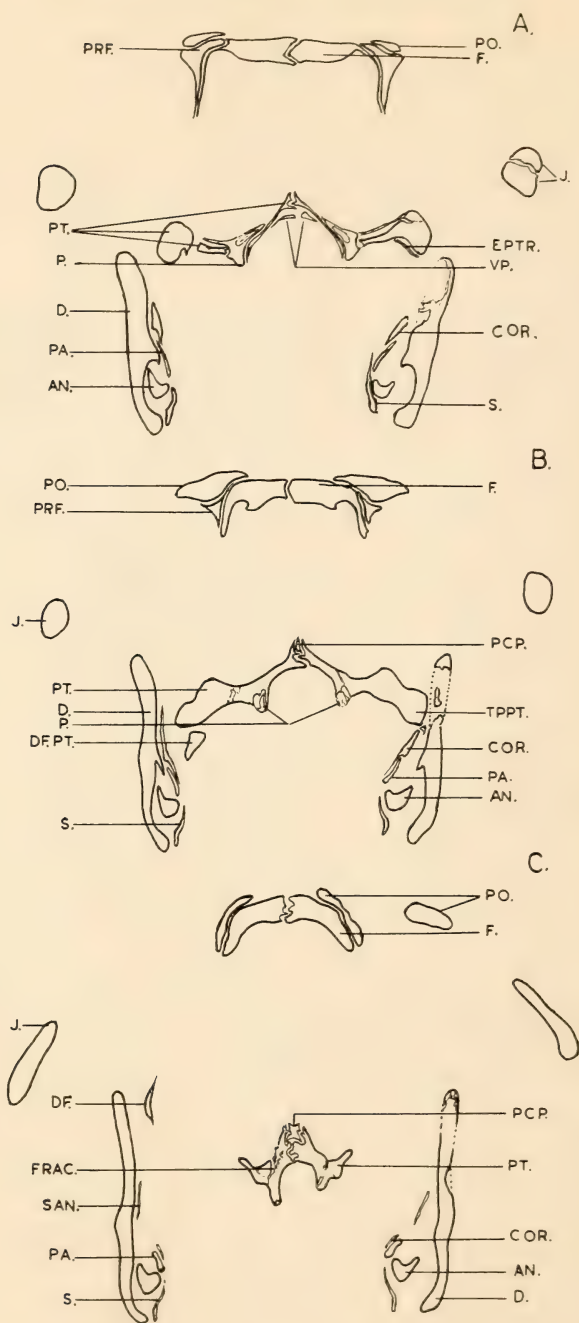


Fig. 15. Transverse sections through skull and lower jaw in orbital region. Note: A. Posterior ends of vomer and ectopterygoids and anterior ends of postorbitals; B. Posterior ends of prefrontals and palatines and anterior end of rostrum of parasphenoid; C. Relationship between pterygoids and parasphenoid rostrum behind transverse processes of pterygoids. A $\times 1,9$. B-C $\times 1,75$.

a cartilaginous internasal and interorbital septum. In the higher cynodonts the interorbital septum is apparently replaced by a presphenoid.

The ventral palatal extensions of the premaxillaries, maxillaries and palatines form a secondary palate. The vertical plate of the vomer lies above the median longitudinal suture of the palate but is not in contact with it. The two halves of the palate meet each other in a *sutura harmonia*. Along the median dorsal margin of each half of the palate runs a distinct ridge (see Figs 8B, 9). The secondary palate is incipient in *Gorgonopsia*, where the anterior end of the vomer is broad and flat.

In *Thrinaxodon* and higher cynodonts the development of the secondary palate is much more advanced than that of *Gorgonopsia*. The transformation of the anterior end of the vomer from a broad flat structure to a vertically orientated sheet of bone and the development of a secondary palate, without which breathing would be difficult when food was chewed, are probably related to the development of homoiothermy. The secondary palate was probably necessary for a proper chewing process, which in turn was probably a prerequisite for quicker liberation of energy from the food taken in. A larger supply of energy was apparently needed in the more active advanced mammal-like reptiles. The enlarged nasal passage resulting from the development of the secondary palate was probably utilized for expansion of the surface of the mucous membrane, since the turbinates, for the presence of which there are indications (see p. 383), were probably rudimentary. Such an increased surface of mucous membrane would have been necessary to moisten and warm the increased supply of air taken in due to increased activity in those animals with increased metabolic rate and incipient homoiothermy.

Brink (1957) discussed the question of homoiothermy and related developments in the advanced therapsids. The nasal passage itself was possibly completely divided (but the nasopharyngeal passage only incompletely) by the vertical plate of the vomer, the probable internasal septum which appears to have rested in the groove on the dorsal edge of the vertical plate of the vomer, and an indeterminate structure between the lower end of the vomer and the palate. Possibly the ridge along the median dorsal edge of each half of the palate and the thickened lower margin of the vertical plate of the vomer indicate the attachment areas of a strong connective tissue connection between these structures.

Pterygoid (Figs 1, 6, 14B–17C)

Sectioning has revealed a considerable amount of additional information about the pterygoids. The antero-medial portion of each pterygoid is overlapped ventrally by the horizontal plate of the vomer (Figs 1, 14B, VP, KVP, PT), and the antero-lateral portion is overlapped dorsally by the palatine (Figs 14B, 15A, P, PT). It may be noted here that the structures indicated by Broom (1938a, fig. 9) as pterygoid and maxillary, are really the palatine and pterygoid respectively.

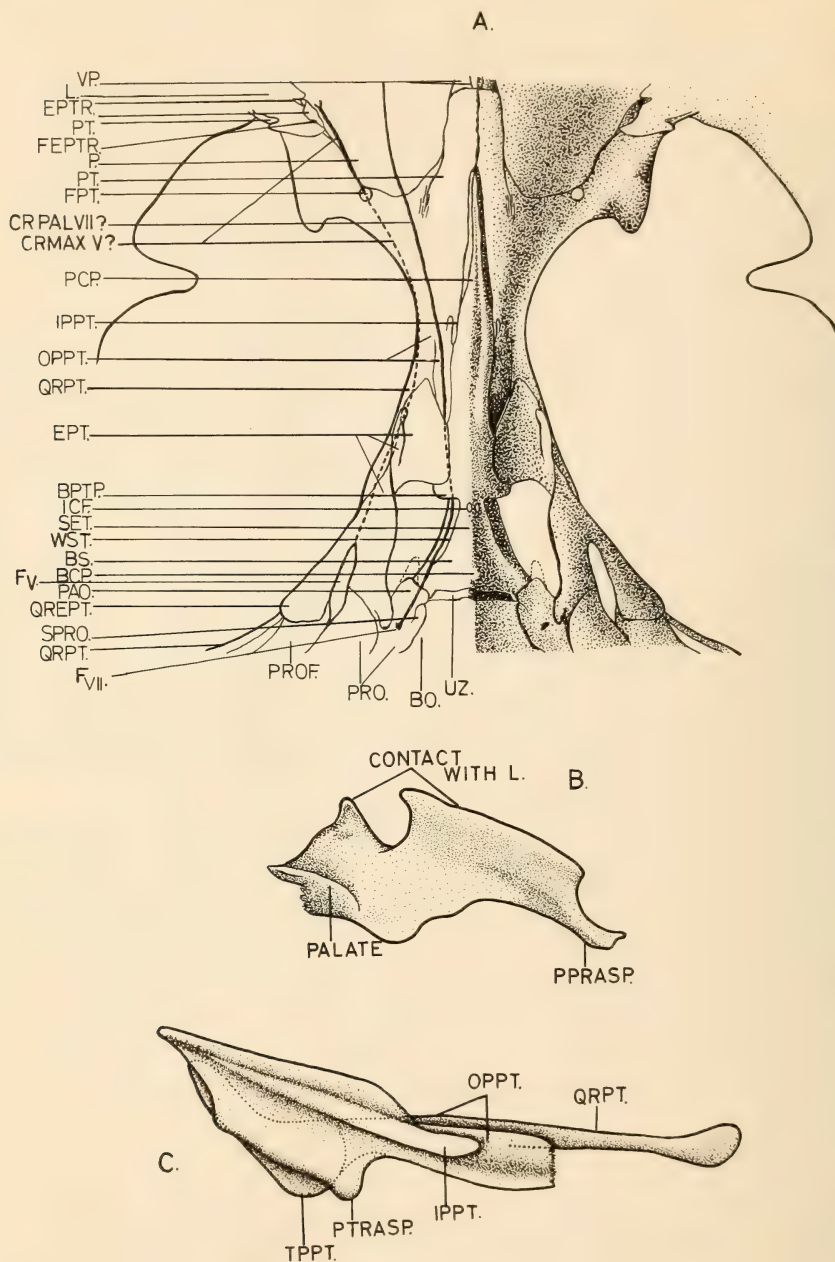


Fig. 16. Graphic reconstructions of: A. Part of palate and basicranium in dorsal view; B. Medial view of palatine; C. Medial view of pterygoid. $\times 2,5$.

The relationships of the pterygoids with the other basicranial elements behind the transverse processes of the pterygoids which guide the lower jaw (Figs 15B, 16C, TPPT) are of considerable interest because of the nature of their sutures with the parasphenoid and epipterygoids. The rostrum of the parasphenoid (Figs 15B, C, 16A, 17, PCP) lies between the posterior extensions of the pterygoids. These extensions have interdigitated sutures with each other and with the rostrum (Figs 15, 17, PT, PCP). Fractures reveal a similar condition in cynognathid skulls investigated by the present author. At the level where the anterior part of the rostrum appears in ventral view, each pterygoid divides into two bars (Fig. 17A, IDIOPPT; Figs 1, 16A, C, 17B, C, IPPT, OPPT).

Estes (1961) indicates very distinct interpterygoid vacuities at this level in juvenile *Thrinaxodon* skulls and suggests that in older specimens these vacuities are obscured by appression caused by their stronger pterygoid musculature. It is possible that the vacuities described by Estes are not natural structures, since he states that both the juvenile skulls investigated by him were crushed dorso-ventrally, which may have been responsible for the formation of 'interpterygoid vacuities'.

The inner bars (IPPT) which are joined to the rostrum by interdigitated sutures (Fig. 17B) extend back for 5 mm (Figs 1, 16C). Broom (1938, fig. 12) mistook these inner bars for the epipterygoids. In a posterior direction the inner bars taper to points which fit into shallow pits in the rostrum of the parasphenoid (Fig. 17C) exactly as described by Olson (1944). About 1.5 mm behind the division of the pterygoid, the outer bar (OPPT) widens outwards and upwards to support the anterior ventral tip of the epipterygoid (Figs 1, 16A, 17B, EPT) which rests in a groove on this outer pterygoid bar. In section this tip of the epipterygoid rapidly expands in a posterior direction to form a distinct antero-ventral process of the epipterygoid (see Fig. 22). This part of the epipterygoid appears to agree closely with the same structure in *Oligokyphus* (Kühne 1956: 55, pl. 10, fig. 1b).

The widened outer pterygoid bar divides into two about 5 mm behind the initial division of the pterygoid into an inner and an outer bar. The quadrate ramus of the pterygoid (QRPT) separates from the dorso-lateral part of the outer pterygoid bar (Figs 1, 16A, C, 17C). The remaining median part of the outer pterygoid bar extends back only 1 mm behind the division before it meets the basisphenoid in a serrated suture (Fig. 1, PTPSS).

Parrington (1946) describes ridges on the ventral surfaces of the pterygoids which continue on to the basisphenoid. The present investigation shows that a ridge extends backwards from the posterior part of each palatine, on to the pterygoid and finally on to the basisphenoid. The anterior palatine-pterygoid part of the ridge (Fig. 1, PPRASP) has been described as a ridge for the attachment of the soft palate, an identification which should probably be extended to include the more posterior part of the ridge formed by the pterygoid only (PTRASP), but this interpretation results in the assumed presence of a very long, soft palate. The pterygoid part of each ridge is formed by the median

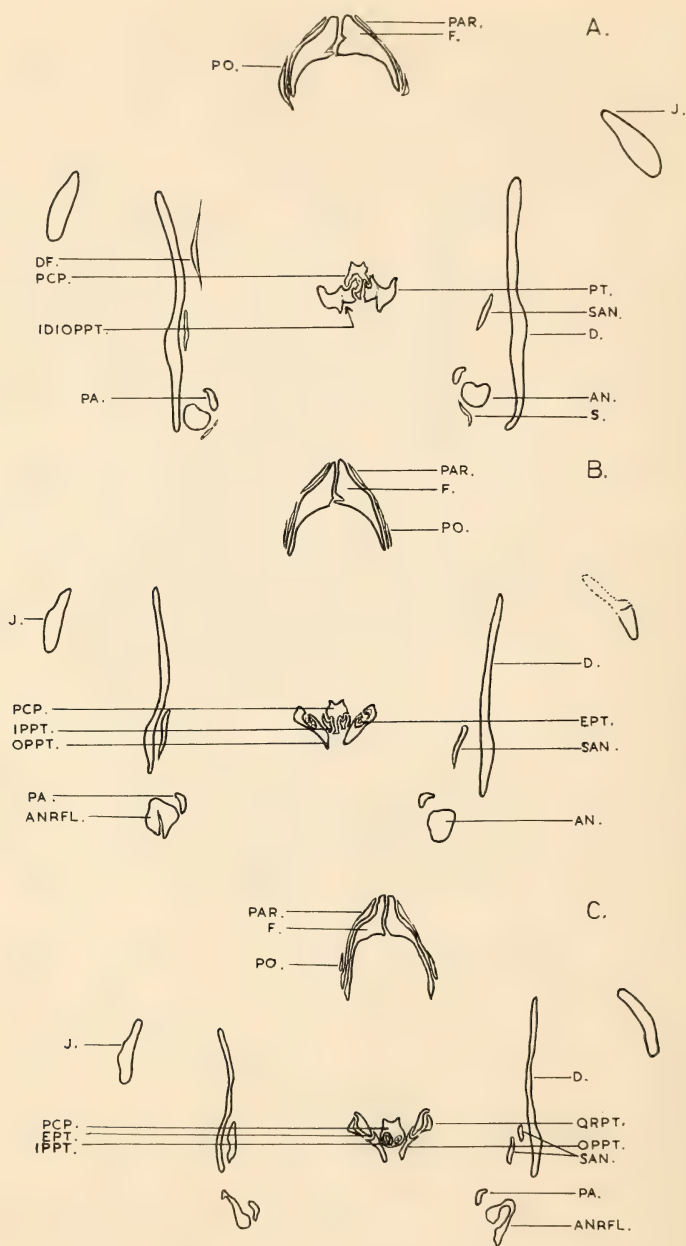


Fig. 17. Transverse sections through skull and lower jaw showing relationships: between frontals, parietals and postorbitals; between pterygoids, epipterygoids and parasphenoid rostrum; between elements of lower jaw.

A $\times 1,8$. B $\times c 1,7$. C $\times 1,5$.

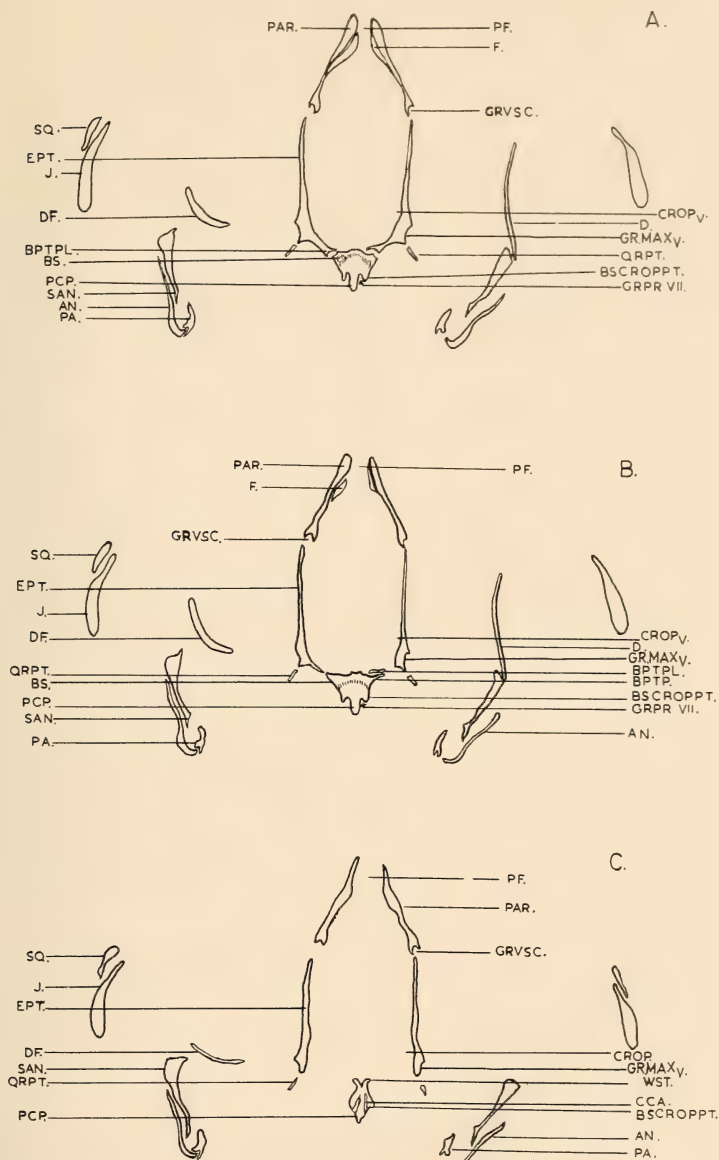


Fig. 18. Transverse sections through braincase and lower jaw showing parietal foramen, relationships between parietals, epipterygoids and basi-sphenoid and between carotid canals and sella turcica. Note surangular, angular and prearticular relationships. $\times 1.5$.

ventral part of the outer pterygoid bar and its posterior end by a ridge on the basisphenoid (Figs 18A, B, C, BSCROPPT) just lateral to the keeled posterior part of the parasphenoid rostrum (see Fig. 1). The basisphenoid part of the ridge forms the median ventral margin of the basiptyergoid process (Fig. 1, BPTP).

Between the keeled posterior part of the parasphenoid rostrum (Parrington's (1946) 'ridge on the processus cultriformis') and the closely applied median ventral part of the outer pterygoid bars, deep grooves are formed. These grooves continue backwards on to the ventral surface of the basisphenoid (Figs 1, 18A, B, GRPR_{vii}) as far as the internal carotid foramina (Fig. 1, ICF). Olson (1944) suggested that the rami palatini of the facial nerves passed forward in these grooves and then turned upwards between the pterygoids and basisphenoid, anterior to the basiptyergoid processes. Parrington (1946) questioned this suggestion because he thought that Olson did not show clearly where the nerve re-entered the skull. This uncertainty apparently rests on a misunderstanding of Olson's description. The point of re-entry could lie in the fork between the inner pterygoid bar (suturally joined to the rostrum) and the outer pterygoid bar (Figs 1, 16A) in what may be, according to the description of Estes (1961), the remnant of the interptyergoid vacuity. The canal is difficult to see without sectioning, because the ventral parts of the outer pterygoid bars are inclined towards each other (Fig. 17B, C, OPPT). A similar condition exists in the cynognathids which were investigated. In these forms the probable course of the ramus palatinus of the facial nerve can easily be followed forward from its exit from the braincase.

Parrington (1946) suggested that a small foramen which he found only in one specimen on the left side between the basiptyergoid process and the pterygoid might have transmitted the ramus palatinus. The actual relationships between the bones, as determined by sectioning, differ somewhat from those figured by Parrington, and the foramen probably represents a small opening in the suture between the two elements.

Probably the ramus palatinus of the facial nerve passed through the pterygoid-parasphenoid canal described above (Fig. 16A, CRPAL_{vii}). From here it may have passed backwards lateral to the internal carotid foramina, on to the upper half of the lateral face of the basisphenoid. In the region of the unossified zone it may have passed on to the concave lateral face of the prootic on which it probably ran gradually upwards. It probably passed below the lateral lamina of the prootic (PROF) and entered its foramen which is situated just below and behind the large foramen for the trigeminal nerve. The maxillary ramus (Figs 1, 16A, CRMAX_v) of the trigeminal nerve after leaving the 'maxillary antrum' probably continued in the groove on the dorsal surface of the pterygoid until it penetrated the foramen pterygoideum (FPT). From here it probably continued along the latero-ventral surface of the outer prong of the pterygoid (OPPT) until the latter's quadrate ramus (QRPT) separated and the antero-ventral process of the epiptyergoid became laterally exposed. From this point the

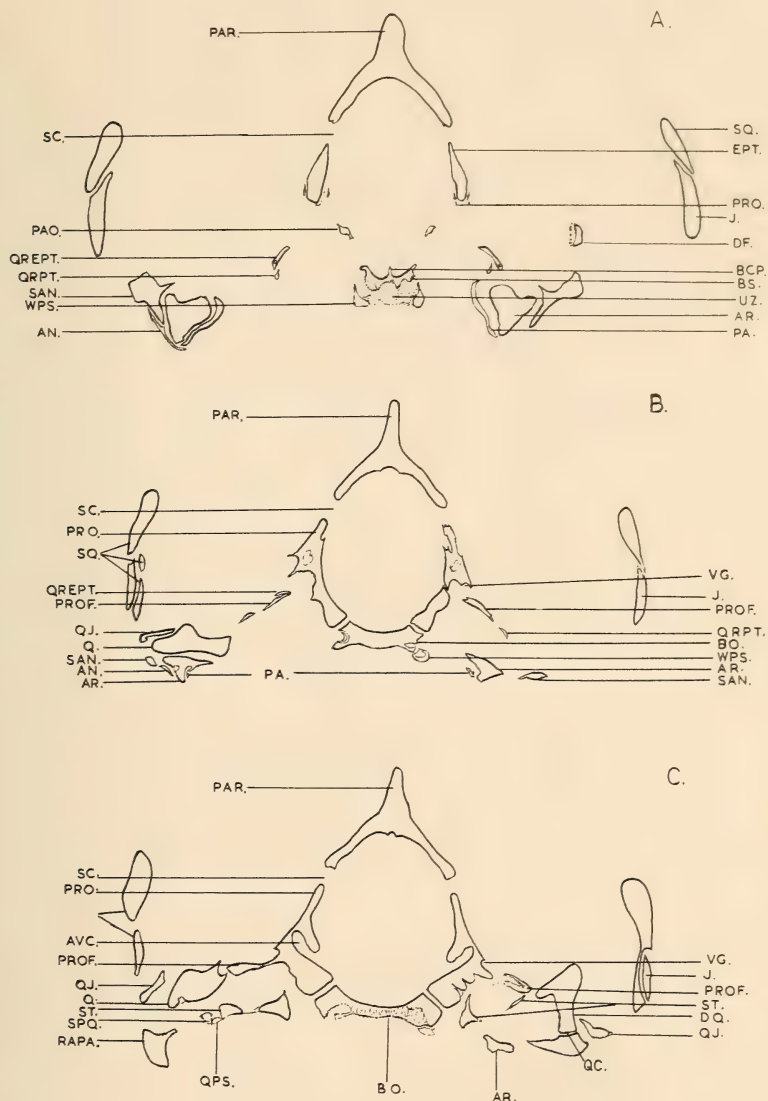


Fig. 19. Transverse sections through braincase and lower jaw. A. Trigeminal foramen, tips of pila antotica and antero-dorsal process of prootic and unossified zone in basicranium. B. Suspensorial region and lateral lamina of prootic. C. Retroarticular process of articular, anterior vertical semicircular canal of internal ear, and relationships between lateral lamina, quadrate and stapes.

A $\times 1.7$. B-C $\times c. 1.5$.

maxillary ramus probably continued along the groove (Fig. 18, CRMAX_v) on its surface, just above the level of the quadrate ramus of the pterygoid, until it reached the ganglion Gasseri lying within the foramen (F_v) between the epipterygoid and prootic (Figs 1, 16A). The abducent nerve probably followed much the same course as the palatine ramus of the facial nerve and entered its foramen (Fig. 6A, F_{vi}) anterior to and below the foramen for the former. The geniculate ganglion of the facial nerve (VII) probably lay in the posterior part of the foramen between the epipterygoid and the prootic, in a recess under the prootic. After entering its foramen the palatine ramus of the facial nerve had only to run directly upwards for a very short distance before joining its ganglion.

Basisphenoid and parasphenoid (Figs 1, 6, 15B–16A, 17A–19B, 20, 21C, 22B, 25A, 28, 29A)

Sectioning revealed no more information than that given by Olson (1944) and Parrington (1946), and that given above under the section on the pterygoid. An unossified zone is present between the basisphenoid and basioccipital (Figs 1, 6A, 16A, 19A, 20, UZ). The parasphenoid is well developed laterally. Earlier preparation of the sectioned skull exposed the basicranium so that it is not possible to be sure exactly how far the parasphenoid extends backwards on the ventral surface. It does not cover the unossified zone and the anterior part of the basioccipital, but this may be due either to damage or to the fact that the specimen is fairly young (Fig. 1, WPS).

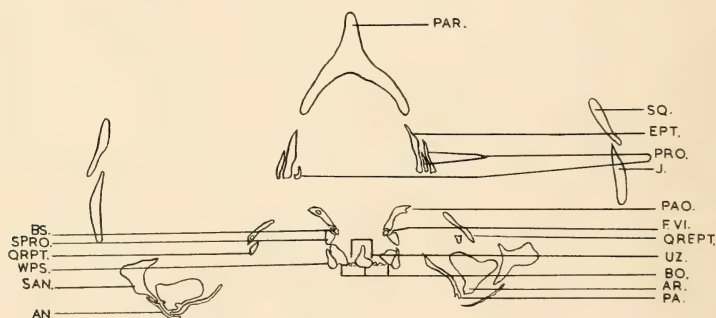


Fig. 20. Transverse section through braincase and lower jaw showing relationship between epipterygoid and prootic, abducent foramen (see also Figs 21C and 24A), and unossified zone in basicranium. $\times 1,5$.

In ventral view the wings of the parasphenoid do not extend as far laterally towards the fenestra ovalis as they are figured by Parrington (1946). Again the difference may be ascribed to different stages of growth, since Estes (1961) also figures the posterior ends of the wings of the parasphenoid in very young specimens as lying comparatively farther forward than shown by Parrington. The dorsum sellae is practically non-existent and therefore the sella turcica (SET) is very shallow and narrow and flanked laterally by thin bone walls

(Figs 16A, 21C, SET, WST). The internal carotid canals emerge almost directly above their points of entry into the parasphenoid-basisphenoid (Figs 1, 16A, ICF; 18C, CCA).

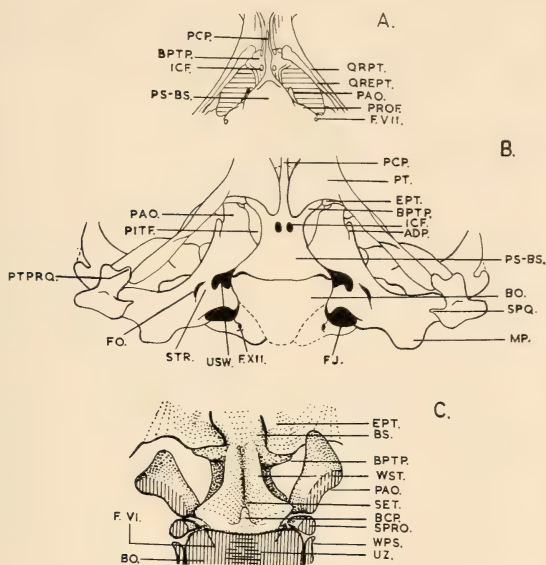


Fig. 21. A. Ventral view of part of basicranium (after Parrington 1946) showing pila antotica and basipterygoid process. B. Ventral view of basicranium of a scalloposaurid (after Crompton 1955*b*) for comparison with A. C. Postero-dorsal view into braincase of enlarged wax reconstruction of serially sectioned skull showing shallow sella turcica, basicranial process, abducent foramen and pila antotica. C $\times 2.5$.

The parasphenoidal teeth described in juvenile *Thrinaxodon* specimens by Estes (1961) may be similar to the irregular surface of the thickened medio-ventral margin of the maxillary and palatine in cynodonts. The median bony ridge thus formed appears comparable with the raphe palati of the mammalian palate. Seeley (1908) described the irregular surface of the maxillary and palatine as a dental armature and Watson (1911) referred to granules with enamelled tips. Broom (1911) and Broili & Schröder (1934*a*) rejected these descriptions. The present author regards the irregular surface of the median ridge as part of the attachment for a mucous membrane which had to be firmly fixed so that forceful movements of the tongue would not dislodge it. In mammals the lamina propria of the mucous membrane is usually continuous with the periosteum of the bone above. Laterally the mucous membrane is not evenly adherent to the bone and is connected to it by strong bundles of connective tissue. The epithelium of the hard palate, which has to be able to withstand wear and tear, is

attached to the median 'raphe' by a thin lamina propria. Rugae with connective tissue cores radiate laterally from the raphe, the uneven surface of which may serve to aid in the attachment of the connective tissue cores (to the periosteum).

A small foramen, described by Estes (1961) and confirmed by the current investigation, lies in each wing of the parasphenoid just medial to the fenestra ovalis and anterior to the opisthotic contact with the basioccipital (Figs 1, 25A, FN₁). This foramen is situated in the precise position where the mammalian Eustachian tube opens.

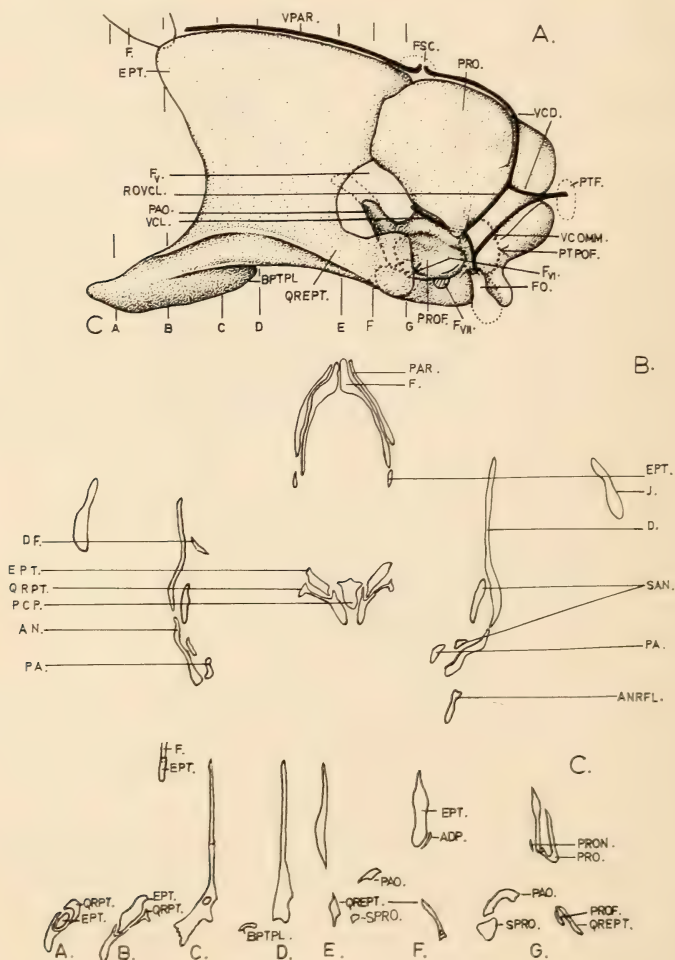


Fig. 22. A. Graphic reconstruction of epipterygoid and prootic in lateral view to show probable system of veins, contact with frontal, and levels of sections given in C. B. Transverse section showing frontal-epipterygoid contact, detaching quadrate ramus of pterygoid and postdentary bones of lower jaw. C. Sections indicated in A. A $\times 3$. B $\times 1.5$. C $\times 2.1$.

Epipterygoid (Figs 1, 6A, B, 16A, 17B-19B, 20-22, 28)

The only feature of this bone which has not been described in earlier publications is the relationship of the tip of its antero-ventral process to the pterygoid, described above under Pterygoid (p. 359). The slight overlap of the frontal and epipterygoid (Figs 1, 6A, B, 22A, B, C) is a feature also found in the cynognathid skull and it is described by Crompton (1958) in *Diarthrognathus* as well. In *Thrinaxodon* the anterior part of the lateral flange of the frontal is laterally overlapped by the prefrontal (Figs 6, 15A, B, F, PRF). The anterior part of the postorbital in turn partly overlaps the posterior end of the prefrontal, but actually lies mainly dorsal to the bone (Fig. 6B, PO, PRF). Further back the lateral flange of the frontal is laterally overlapped by the thin front end of the parietal of which the lower part in turn is laterally overlapped by the posterior end of the postorbital (Figs 6, 17, PAR, PO). Between the posterior end of the prefrontal and the anterior end of the parietal only the postorbital overlaps the frontal flange. Behind the postorbital only the thin parietal sheet overlaps the frontal flange (Figs 6, 18A, B). At this level the frontal forms the anterior and lateral lower margins of the wall of the parietal foramen (PF). In sections the posterior lower part of the lateral flange of the frontal anterior to the parietal foramen becomes progressively longer, until its lower end makes contact with the anterior upper edge of the epipterygoid (Figs 6, 22, F, EPT). This ventrally projecting part of the frontal ends well in front of the upper part of the bone and the parietal foramen. In this region the lower end of the frontal flange protrudes well below the parietal which overlaps its dorsal part (Fig. 6B).

Sectioning, therefore, shows that it is not just a slender horizontal process of the frontal which meets the epipterygoid. The median wall of the orbit is formed in the same way in the cynognathids and *Diarthrognathus*, and closely resembles the condition in mammals and tritylodontids.

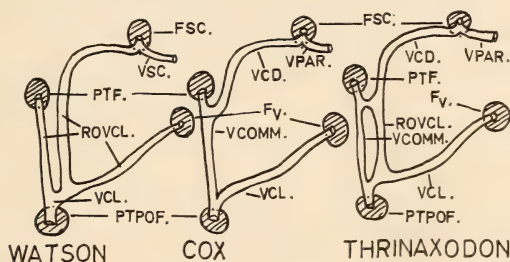


Fig. 23. Three diagrams to show various interpretations of venous system around braincase. $\times c. 2.5$.

Prootic (Figs 1, 2, 6, 16A, 19A-22A, 22C-24A, 25A, 26, 27, 29A, B)

The anterior part of the prootic consists of the antero-dorsal process (ossified taenia marginalis, Crompton 1955b) which forms the postero-dorsal margin of the trigeminal foramen (Figs 22A, 24A, ADP), and the antero-ventral process, identified by Parrington (1946) and Crompton (1955b) as an

ossification of the pila antotica (PAO) which forms the postero-ventral margin of the trigeminal foramen. The postero-dorsal part of the epipterygoid, which forms the antero-dorsal margin of the trigeminal foramen, projects on to the anterior part of the antero-dorsal process to which it is joined by a serrated suture. It is held between a large outer plate and a slender inner process (Figs 6A, 22A, 28, ADP). The notch described by Olson (1944: 16-17), dorsal to both the prootic incisure and the latero-dorsal process, is closed off by the lower margin of the parietal to form the foramen for the vena capitis dorsalis (Figs 6A, 22A, FSC) (see also pp. 373-5).

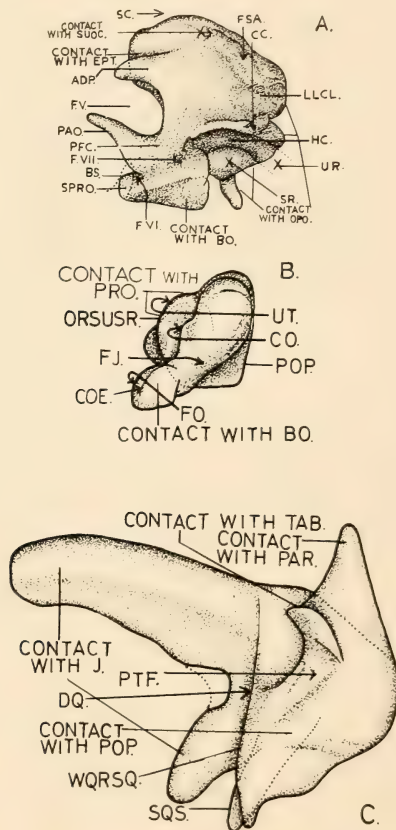


Fig. 24. Graphic reconstructions of medial views of: A. Prootic; B. Opisthotic; C. Squamosal. $\times 2,5$.

Some detail can be added to the descriptions by Olson (1944) and Parrington (1946) of the foramen for the abducent nerve. The nerve passes through a deep notch in the antero-ventral edge of the antero-ventral process (pila antotica) (Figs 20, 21C, 24A, F_{vi}). The notch is closed anteriorly by a postero-dorsally

directed flange of the lateral wall of the sella turcica which lies in the dorsal surface of the basisphenoid (Figs 6A, 16A, 21C, BS, WST, F_{vi}). Olson's (1944) figure is therefore more closely comparable with the structure as determined in the present investigation than Parrington's (1946) figure in which the foramen lies entirely within the antero-ventral process.

Sectioning shows that the foramen lies behind the sella turcica and the unossified zone. The foramen for the facial nerve (Figs 24A, 27, 28, F_{vii}) is quite distinct immediately below and behind the prootic incisure (posterior wall of the trigeminal foramen) from which it is separated by the prefacial commissure. The ramus ophthalmicus profundus of the trigeminal nerve probably ran forward along the medial surface of the lower third of the epipterygoid from the Gasserian ganglion lying just within the trigeminal foramen. Its possible course is indicated by a slight though definite groove on the medial surface of the epipterygoid just above the level of the antero-ventral process of this bone. On emerging from the braincase through the lower end of the foramen lacerum anterium (Fig. 6A, FLA), the ramus ophthalmicus profundus would have been immediately above the anterior ventral part of the epipterygoid (Fig. 18, $CROP_v$) which is in contact anteriorly with the pterygoid, and more posteriorly with the basisphenoid (Fig. 18B, BPTPL).

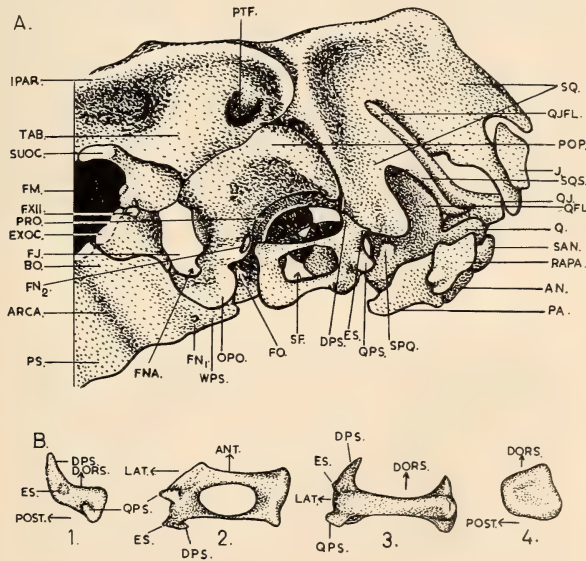


Fig. 25. A. Antero-ventral view of posterior part of enlarged wax reproduction of serially sectioned skull to show contacts of stapes and quadrate. Note retroarticular process of articular. B1, 2, 3, 4. Lateral, ventral, anterior and medial views of right stapes. Note positions of anterior, dorsal and posterior planes in the different views. $\times 2.5$.

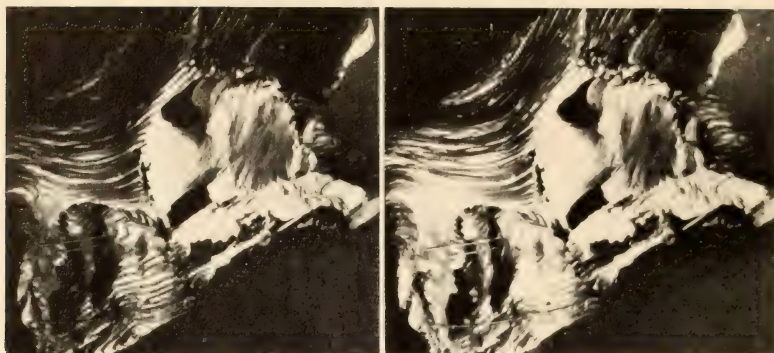


Fig. 26. Stereophotograph of anterior view of right posterior part of model of serially sectioned skull showing squamosal recess with quadrate and quadratojugal, as well as outer surface of prootic with grooves and canals for system of veins. Approximately $\times 3$. (See also Fig. 22A.) See accompanying diagram for lettering.

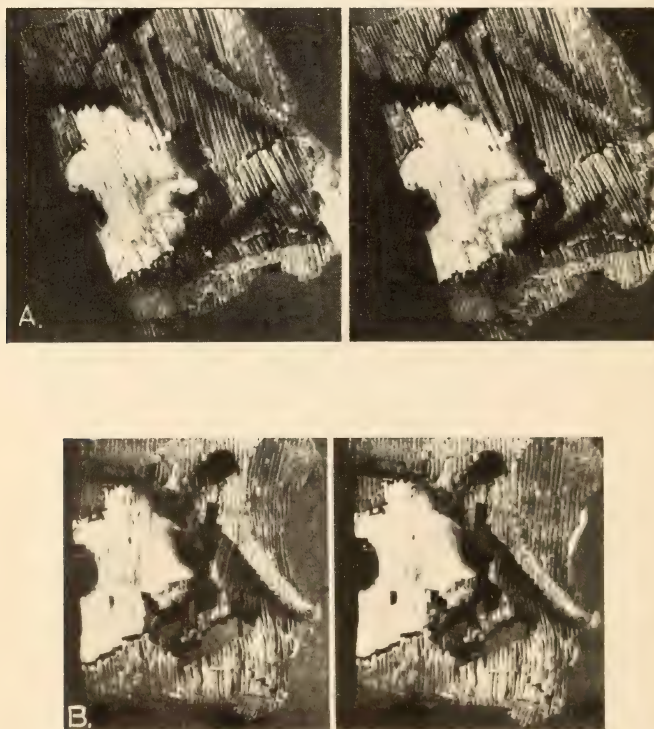


Fig. 27. Stereophotographs of: A. Inner surface of wall of right side of braincase; B. Floor and ventrally situated structural features (jugular foramen, sacculo-cochlear recess and fenestra ovalis). Approximately $\times 2.5$. See accompanying explanatory diagrams for lettering. (See also Figs 24A, 28.)

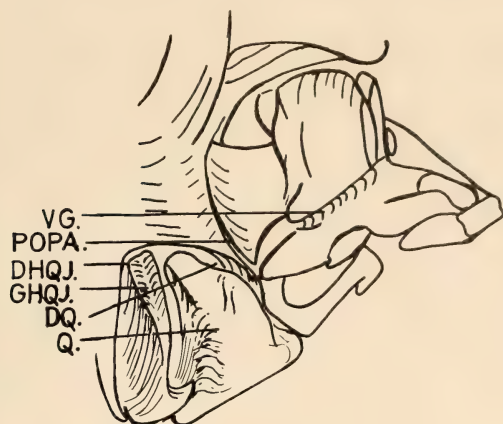


Fig. 26. Explanatory diagram.

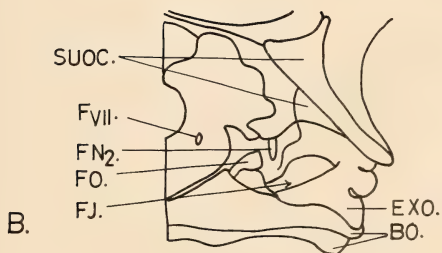
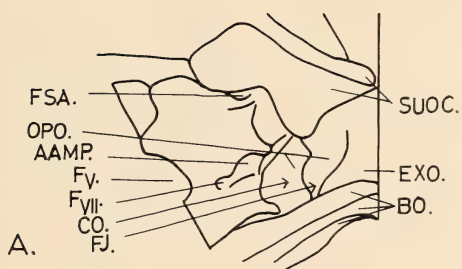


Fig. 27. Explanatory diagram.

The paroccipital process is formed by a postero-lateral flange of the prootic (see Fig. 26) which rests dorsally on the opisthotic in a squamous suture (Fig. 29B, PRO, POP, OPO). It abuts against the squamosal with only its dorsal and ventral margins, but possibly had a cartilaginous cap which became ossified during later stages of growth than that represented by the sectioned skull. The step-like suture described by Parrington, between the prootic and opisthotic (Figs 1, 25A, POP, PRO) which forms part of the roof and the hind wall of the middle ear cavity, is confirmed. The prootic flange (lateral lamina) (PROF) forms the anterior border of the pterygo-paroccipital foramen (Fig. 2, PTPOF) and meets the quadrate rami of the pterygoid and epipterygoid (Figs 1, 2, 16A, 19B, 22A, QREPT). The lateral lamina of the prootic and the quadrate ramus of the pterygoid extend to the median margin of the quadrate (Figs 1, 17C, 26, Q).

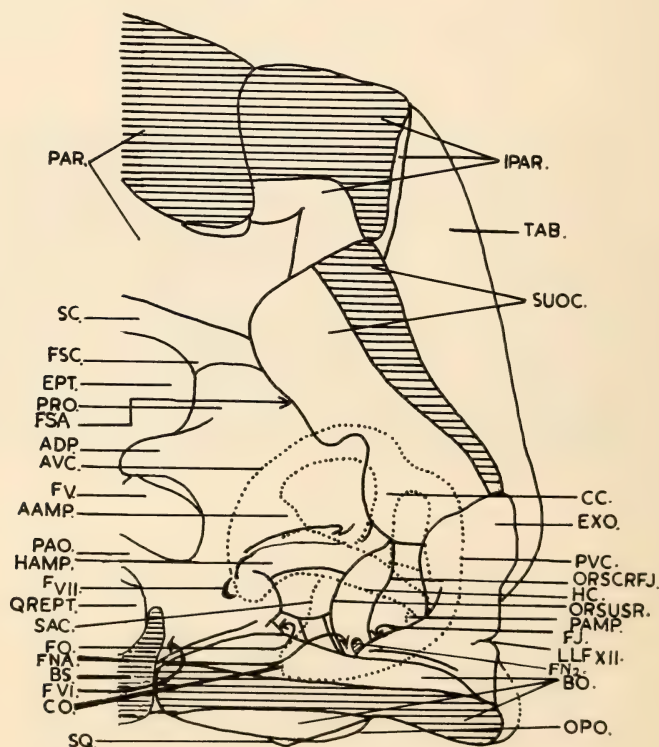


Fig. 28. Graphic reconstruction of inner ear structures in relation to the otic and occipital bones. $\times 4$.

The subarcuate fossa is very distinct (Figs 24A, 27, 28, FSA). In an oblique dorsal view backwards into the braincase this excavation for the lateral lobe of the cerebellum appears to extend into a large space above the anterior opening

of the posttemporal fossa. There appears to be no vascular duct which penetrates the cranial wall from the subarcuate fossa as there is in *Oligokyphus* (Kühne 1956). (See, however, under Supraoccipital, p. 378.) A convexly curved horizontal lamina separated the excavation for the lateral lobe of the cerebellum from the horizontal canal and the vestibule (Fig. 27A). This lamina is also described by Brink (1955a, fig. 2b) for *Diademodon*, in which the conditions in this part of the braincase agree very closely with those in *Thrinaxodon*. The relationship of the semicircular canals to the subarcuate fossa can be seen in Figure 28.

The most interesting feature of the otic bones is the system of grooves, canals, and foramina for veins which enter and leave the braincase and was described by Watson (1920) and Parrington (1946). In a study of the dicynodont *Kingoria*, Cox (1959) pays considerable attention to these veins. Since the system of grooves, canals, and foramina in *Kingoria* appears to be closely comparable with that of *Thrinaxodon* and of the cynognathids, Cox's interpretations, with those of the earlier investigators, are of considerable value for understanding the conditions in *Thrinaxodon*. Cox suggests that the groove (Fig. 18, GRVSC) along the junction of the parietal and epipterygoid of cynodonts represents the course of the vena parietalis, and the foramen (Figs 6A, 22A, 28, FSC, 26, 27) described by Watson (1911, 1920) between the parietal and prootic is the point of entry into the braincase of the vena parietalis and the vena capitis dorsalis (Watson's 'vein of sinus canal') which, according to Cox, drained forward from the occipital musculature. The course of this latter vein was through the posttemporal fossa, then upwards into the posterior end of the dorsal groove (sinus canal), and into the braincase through the above-mentioned foramen. The vena capitis lateralis ran between the pterygo-paroccipital foramen (Figs 22A, 23, PTPOF, 26) and the trigeminal foramen. The vena capitis dorsalis and the vena capitis lateralis were joined by a vein which ran forward across the dorsal and anterior surfaces of the paroccipital process from the posttemporal foramen into the pterygo-paroccipital foramen, to provide an alternative method of drainage. Cox's interpretation is a modification of Watson's (1920) and is supposed to allow for the fact that the vein which occupied the posttemporal fossa drained forward.

In Watson's interpretation, which is made difficult because it gives a wrong impression of the direction of flow of the blood, the vena capitis lateralis ran through the pterygo-paroccipital foramen and was formed by three roots. These were: one which ran forward through the posttemporal fossa; one which ran backwards from the trigeminal foramen; and one which ran backwards in and then downwards and forwards from the 'sinus canal' which is the groove along the ventral parietal and dorsal prootic and epipterygoid borders. Watson also described two smaller veins. The first is said to have left the braincase through a foramen between the prootic and parietal and then to have joined a vein which ran in the 'sinus canal'. According to Cox this foramen is for the vena parietalis and the vena capitis dorsalis. The second small vein described by

Watson is said to have left the braincase through the upper part of the foramen for the trigeminal nerve and then to have joined the third root of the vena capitis lateralis which ran from this same foramen.

A study of the skull of *Thrinaxodon* reveals that the grooves and canals fit the interpretation of Watson (1920) of the courses of the main veins as well as they do that of Cox (1959) and that the correct interpretation may be a synthesis of the two interpretations. Figure 26 shows a very distinct groove (VG) running between the pterygo-paroccipital foramen and the trigeminal foramen. Both Watson and Cox agree that a vein ran along this groove, Watson calling it a root of the vena capitis lateralis, and Cox calling it *the* vena capitis lateralis. The structure of the anterior dorsal face of the paroccipital process leaves no doubt that a vein ran across it (see Fig. 26) between the posttemporal fossa and the pterygo-paroccipital foramen. This vein must have been the second root of the vena capitis lateralis described by Watson and which is regarded by Cox as a communicating vein between the vein which he calls the 'vena capitis dorsalis' and the vein which he calls the 'vena capitis lateralis'.

In order to understand the course of Cox's vena parietalis and vena capitis dorsalis, and Watson's vein of the sinus canal, it is necessary to describe briefly the relationship between the lower margin of the parietal and the upper margins of the epipterygoid and prootic.

In the reconstructed skull of *Thrinaxodon* the parietal and the epipterygoid do not make contact and the anterior part of Watson's sinus canal is therefore not distinct (Fig. 6A, EPT). Since the lower margin of the parietal is, however, grooved (Fig. 18, GRVSC) it is possible that the epipterygoid and the anterior part of the prootic are slightly dislocated from the parietal, or else that further growth would have formed the groove or canal proper. The posterior part of the groove (canal) is normal in the reconstructed skull where it is walled medially by the anterior end of the supraoccipital (Figs 6A, 29A, SUOC).

Watson believed that a third root of the vena capitis lateralis ran along this groove, but Cox believes that its anterior part was occupied by the vena parietalis and its posterior part by the vena capitis dorsalis. The further course of the vein which occupied the posterior part of the groove (or canal) can easily be followed in the reconstructed skull where a distinct groove runs straight downwards from the horizontal groove, well in front of the eaves formed by the squamosal over the posttemporal fossa (Figs 22, VCD, 26). It then continues forwards and downwards on the paroccipital process at its proximal end where it is continuous with the wall of the braincase. Watson's description and figure of the course of the third root of the vena capitis lateralis fit the groove described above very well. Cox's description of the upper part of the groove is also correct, because at the base of the vertical part of the groove where it turns forwards there is an equally distinct part of the groove which turns backwards (Figs 23 *Thrinaxodon*, 26) into the posttemporal fossa. This must be the course of the posterior part of Cox's vena capitis dorsalis. There is no doubt that the vein which ran down the paroccipital process (see p. 373) splits from Cox's vena

capitis dorsalis in the posttemporal fossa because their grooves merge into a single large groove.

The reconstructed *Thrinaxodon* skull also distinctly shows that the third root of the vena capitis lateralis (Watson) joined the one from the trigeminal foramen at the termination of the groove (VG) for the latter vein at the dorsal margin of the pterygo-paroccipital foramen where a distinct lamina of the prootic protects the confluence (Figs 22A, 26).

It appears therefore that:

- (a) the upper end of the third root of the vena capitis lateralis with its own root from the posttemporal fossa is Cox's vena capitis dorsalis;
- (b) the lower end of the third root of the vena capitis lateralis which is not recognized by Cox is present;
- (c) the second root of the vena capitis lateralis which came through the posttemporal fossa to the pterygo-paroccipital foramen is the communicating vein of Cox, and
- (d) the first root of the vena capitis lateralis which ran towards the trigeminal foramen is the vena capitis lateralis of Cox.

The interpretations of Watson (1920), Cox (1959) and the present one for *Thrinaxodon* are compared diagrammatically in Figure 23.

Parietal (Figs 6, 17A–20, 22B, 28, 29)

The relationships of the parietal with the frontal and postorbital have been described above (see Epipterygoid, p. 367). In this region the parietal (PAR) is a thin sheet of bone (Figs 17A–18C). Further back, behind the frontal, the parietal is thicker in section and along its lower end, which almost reaches the upper margin of the epipterygoid, runs the groove for the vena parietalis (Cox 1959) (Fig. 18, GRVSC). Behind the parietal foramen, which is about 4 mm in length, the two parietals are fused and appear in sections as a triradiate structure, the dorsal limb of which forms the parietal crest (Figs 19, 20, 28, 29A, B). Still further back the groove along the lower margin of the parietal disappears. The lower margin of the parietal becomes rounded for a distance of about 6 mm and is separated from the upper borders of the epipterygoid and prootic by an interspace of about 1 mm (Figs 19, 20, 29A) which may be the result of a dislodgement of the bones, or may represent a growth feature which would have disappeared later. Along the posterior dorsal part of the 'sinus canal' between the parietal and prootic the considerably expanded lower end of the parietal and the similarly expanded upper part of the prootic are again distinctly grooved (Fig. 29A, PAR, PRO). In this region the anterior end of the supraoccipital forms the inner wall of the canal (Fig. 26) which now turns downwards and outwards.

Basioccipital and Exoccipital (Figs 1, 6, 16A, 19B–21, 25A, 27–29C)

Very little can be added to the previous descriptions by Olson (1944) and Parrington (1946). Each exoccipital (EXO) meets the supraoccipital (SUOC) in the sectioned skull in a sutura squamosa (Figs 6A, 28). An antero-ventral extension of the exoccipital lies on the latero-dorsal surface of the posterior part

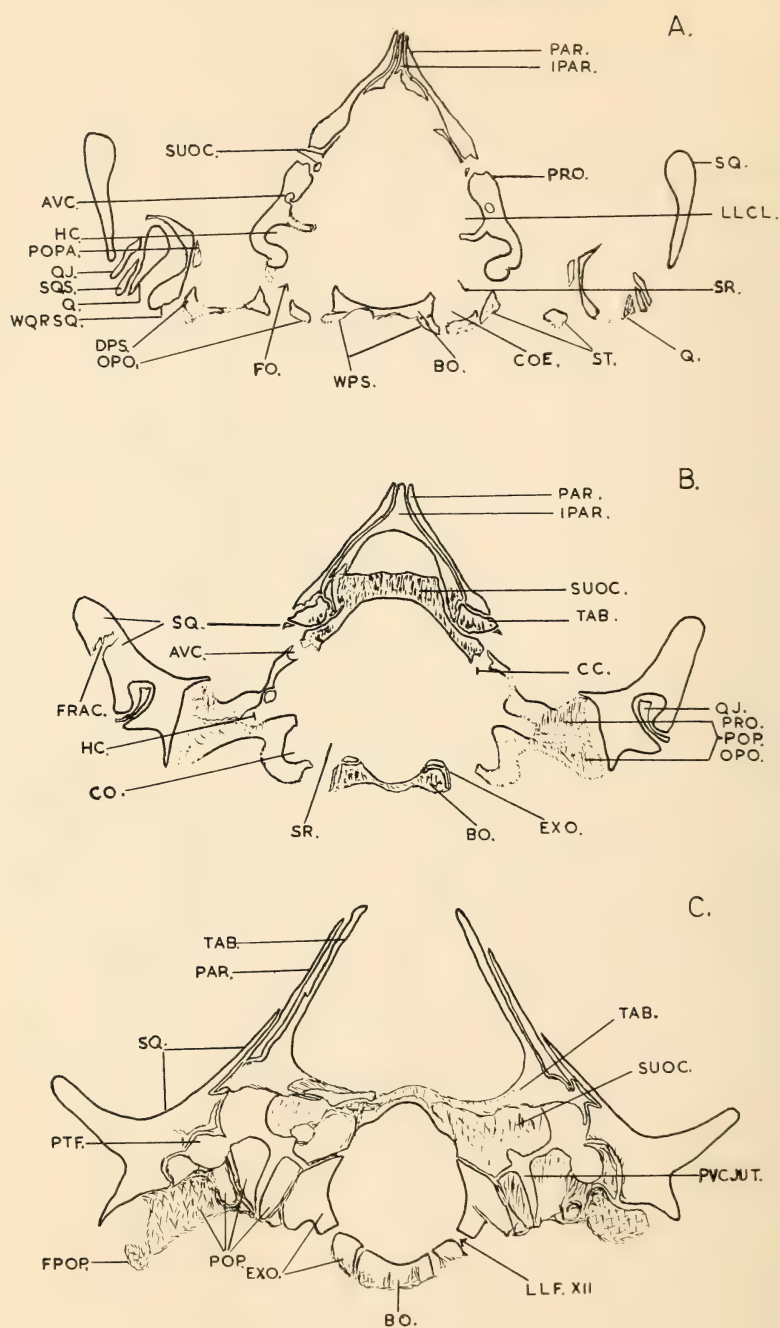


Fig. 29. Transverse sections through posterior part of braincase and occiput to show relationships of constituent bones. Structures accommodating inner ear are indicated. A \times 1,5. B \times 1,6. C \times 2,5.

of the basioccipital (Figs 6A, 27, 28, 29B, C, EXO, BO) where it forms the inner wall of the jugular foramen. Two distinct foramina (Figs 1, 6A, F_{xii}) penetrate the exoccipital. The lower one (LLF_{xii}), which is the larger of the two, leaves the braincase almost in the foramen magnum, and practically below the jugular foramen. The smaller upper foramen lies along the posterior part of the first foramen, but lateral to it, and may have given passage either to a second hypoglossal branch, or to a vein (see Figs 27B, 28).

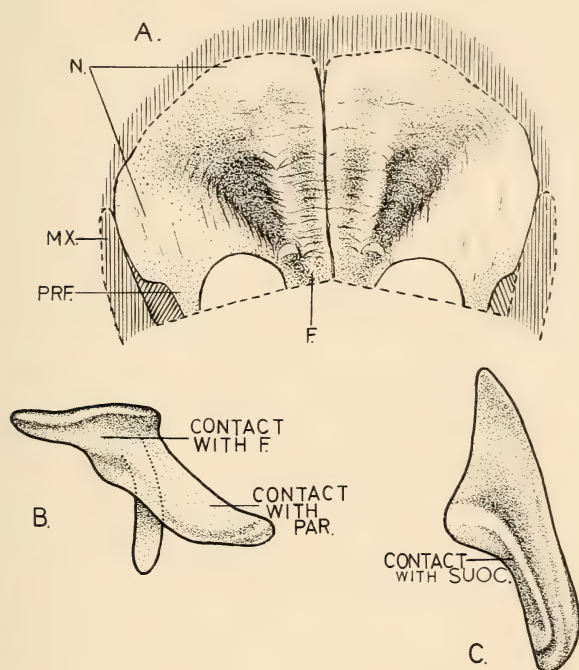


Fig. 30. A. Inner view of roof of snout of enlarged wax reproduction of serially sectioned skull to show series of ridges and depressions probably for attachment of turbinals. B-C. Graphic reconstructions of medial views of postorbital and tabular respectively. $\times 2,5$.

Supraoccipital (Figs 1, 6A, 25A, 27-29)

Mention has been made of the dorso-lateral parts of the supraoccipital (Figs 6A, 28, 29A, SUOC) which extend forward about 2,6 mm beyond the median dorsal shelf on each side of the skull along the upper border of the prootic and the lower border of the parietal. The supraoccipital is a trough-shaped bone which lies tilted back at an angle of about 45 degrees (Figs 6A, 27, 28). The base of the trough forms the roof of the cerebellar part of the braincase and the walls of the trough, which become thicker backwards (Fig. 29A, B), take part in the formation of the walls of the braincase. The anterior upper part of the roof

is considerably expanded in vertical diameter (Figs 6A, 27B, 28). Above this expanded anterior upper end of the supraoccipital, below and in front of the interparietal is an open space about 3 mm in height and about 2 mm in length (Figs 6A, 27B, 28, 29B, IPAR, SUOC). Its maximum anterior width is about 4,5 mm, but it becomes narrower further back. Such a space is also found in the cynognathids investigated, as well as in *Diademodon* (Brink 1955a), but its function is uncertain. Brink suggests that in the live animal a cartilaginous extension of the supraoccipital filled the space. The lower ends of the interparietal come down laterally alongside the expanded anterior part of the supraoccipital shelf (Figs 6A, 28, 29B, IPAR, SUOC) against which they are held by the parietal flanges which completely cover them in lateral view (Figs 6B, 29B, IPAR, PAR). The anterior extensions of the tabulars (Fig. 30C) lie below the lower ends of the interparietal and medio-ventral to the lower ends of the parietals (Fig. 29B, TAB). In lateral view they are exposed for a distance of about 2,2 mm before being covered by the squamosal. This bone forms a roof (Figs 2, SQ, 26) which probably protected the blood-vessels, emerging from the posttemporal fossa, against constricting pressure of the temporal musculature. The anterior exposure of the tabular in the posterior end of the groove for the 'vein of the sinus canal' is also found in the cynognathids and *Diademodon*.

About half-way down its sloping anterior border on each side, the supraoccipital has a wide notch (Figs 6A, 27A, 28, SUOC). This notch is the posterior medial margin of the excavation for the lateral lobe of the cerebellum which is continued postero-laterally towards the posttemporal fossa between the posterior part of the prootic and the supraoccipital. The posterior end of the anterior vertical semicircular canal runs along the notch, but just behind its margin (Fig. 28, AVC). The anterior upper end of the posterior vertical semicircular canal runs in the outer surface of the lower end of the supraoccipital below and behind the notch (Fig 28, PVC). A groove (Figs 6A, 24A, FSA) on the inner upper surface of the posterior part of the prootic is separated from the excavation for the lateral lobe of the cerebellum (LLCL) just below it by a distinct ridge (Figs 6A, 24A, 27A). Medial to it the posterior part of the anterior vertical semicircular canal runs along the margin of the supraoccipital notch (Fig. 29A, B). This groove on the prootic apparently comes from the subarcuate fossa proper and could be the equivalent of the vascular duct described for *Oligokyphus* by Kühne (see p. 373).

The lateral ventral surfaces of the supraoccipital lie on the paroccipital parts of the opisthotics (Fig. 29C, SUOC, POP) and its lower medial surfaces lie on the exoccipitals (Figs 6A, 27, 28, 29C, SUOC, ORSCRFJ, OPO, EXO, POP). These contacts are simple sutura squamosa. On the occiput the lower end of the interparietal overlaps the medio-dorsal part of the supraoccipital and the medial part of each tabular overlaps the lateral dorsal parts of the supraoccipital (Figs 25A, 29C, IPAR, SUOC, TAB). On the occiput the tabular also encloses (Fig. 25A, TAB, PTF) the posttemporal foramen as described by Parrington (1946).

Opisthotic (Figs 1, 6, 24B, 25A, 27–29)

This bone forms the posterior part of the wall of the fenestra ovalis, and the prootic and basioccipital form the anterior part of the wall. The opisthotic separates the fenestra ovalis and jugular foramen of which it forms the anterior and lateral walls (Figs 25A, 27, FO, FJ, OPO). Posteriorly it meets the exoccipital (Figs 6, 25A, 27, 28, 29C, EXO) and postero-dorsally the supraoccipital (Figs 6, 25A, 27, 28, 29C, SUOC). The antero-dorsal part of the paroccipital process is formed by the prootic, and the remaining major part of the process is formed by the opisthotic (Figs 1, 25A, 29B, C, PRO, POP, OPO). The antero-dorsal face of the paroccipital process is excavated probably for the passage of veins (see Prootic above and Fig. 26) and the antero-ventral surface is also excavated to form the middle ear cavity which accommodates the stapes (Figs 1, 25A). The presence of a foramen of unknown significance featured by Estes (1961) and facing laterally in the paroccipital part of the opisthotic about midway between the posterior border of the fenestra ovalis and the antero-median border of the jugular foramen is confirmed (Figs 1, 25A, FN₂). Conceivably the internal jugular vein left the skull through this foramen and not with nerves IX, X and XI through the jugular foramen (foramen lacerum posterium).

Stapes (Figs 1, 19C, 25A, B, 26, 29A)

Both stapes are preserved and in both the stapedia foramen has a central position. Parrington's (1946) figure indicates that the stapedia foramen in his specimen lay more towards the distal end of the stapes. He suggested that in the young form the proximal surface of the head of the stapes was covered by cartilage about 1 mm thick. That the serially ground skull is not that of a fully grown animal is proved by the fact that much larger specimens have been described by other authors. Broom (1938*a*) has described a specimen of 88 mm, while Parrington's (1936*a*) specimen I was 85 mm. The present author has examined two skulls of more than 80 mm in length while the serially ground skull was only 67 mm. (All were measured from the tip of the snout to the end of the parietal crest with the possible exception of Broom's (1938*a*) specimen for which the maximum length may have been given.) It seems, therefore, that the central position of the stapedia foramen must be attributed to the youth of the specimen, and the consequent absence of an ossified cap on the head of the stapes. The proximal end of the right stapes does not quite reach the fenestra ovalis (Fig. 25A, FO), but if a cartilage cap were added it would fit into the cup surrounding the fenestra. A small process at the distal end of the stapes makes contact with the quadrate and this must represent a quadrate process in its correct position. Another even smaller distal process closely approaches the lower end of the groove in the squamosal which housed the external auditory meatus (Figs 1, 25A, B_{1,2,3}, QPS, ES). These processes are so delicate that their preservation can only be expected in an undisturbed stapes. It is therefore concluded that the right stapes is in the correct position and that its proximal end must have been capped by cartilage in life. Conceivably, however, some rotation

might have taken place soon after the death of the animal due to drying and consequent shortening of muscles and ligaments which held the stapes in position in the live animal.

The stapes on the left—although it appears to be in the natural position—has actually been pushed into the cup around the fenestra ovalis by the medial displacement of the quadrate and postdentary bones.

The anterior arm of the stapes (Figs 1, 25A, B_{2, 3}) is distinctly wider and stronger than the posterior arm. A small dorsal process (Figs 1, 25A, B_{1, 2, 3}, DPS), about 1 mm in length, curves upwards and slightly inwards from the posterior corner of the distal end of the stapes, towards the antero-distal end of the paroccipital process. A second process which the present author regards as the quadrate process of the stapes (Figs 1, 25A, B_{1, 2, 3}, QPS) extends ventro-laterally from the middle of the ventro-distal surface of the stapes to meet a similar, but slightly larger process, here called the stapedia process of the quadrate, which extends upwards from the postero-medial surface of the quadrate immediately above the medial part of the condyle (Figs 1, 19C, 25A, QPS, SPQ). A third very small process, here called the extrastapes (Fig 25A, B_{1, 2, 3}, ES), extends laterally from the distal surface of the stapes just in front of the dorsal process. It approaches the lower inner end of the groove in the squamosal for the external auditory meatus very closely. Ossification of the distal region of the stapes and especially of the processes seems to be incomplete, but there can be no doubt about their presence.

There is some difficulty in homologizing these processes with those described by Parrington (1946, 1949). The process here described as the quadrate process of the stapes may, if the stapes had rotated somewhat around its longitudinal axis, be Parrington's extrastapes. The dorsal process gives no difficulty, but the small process at its base, described here as an extrastapes, may conceivably be regarded as part of the dorsal process. The oblique flat face of the stapes at its antero-distal corner above the quadrate process may be regarded as the point of contact between the stapes and the quadrate.

Hopson's description of the *Thrinaxodon* middle ear is essentially correct, but it resembles the tritylodontid condition in structure, and probably function, more extensively than he implies. As in tritylodontids like *Bienotherium*, the stapes would be activated via the quadrate and articular in any jaw opening movement, but the function of this mechanism is unknown although it is a preadaptation to the mammalian condition.

Quadrate (Figs 1, 19B, C, 25A, 26, 29A, 31C, D)

Parrington (1946) described this bone very well and the present investigation largely served to corroborate his description. A foramen which he found in the quadrate '... median to the central thickening and a little way above the articulating surface' appears to be that of a small canal (Fig. 19C, QC) found in the displaced left quadrate. The canal runs transversely through the central thickening of the quadrate. In the intact quadrate this canal emerges on its lateral face

just behind the medio-dorsally directed process at the ventral edge of the quadratojugal. In its normal position (Fig. 26, Q) the quadrate lies in a pocket (Fig 26, DQ) in the anterior face of the squamosal where it is held very loosely. The quadrate has a posteriorly directed flange which fits into a deep notch in the ventral border of the squamosal (Fig. 25A, QFL).

Olson (1944) and Parrington (1946) described a stapelial process of the quadrate (Figs 1, 25A, SPQ) which makes contact with a process of the stapes (see p. 379, Stapes). These authors have also shown that the posterior tips of the quadrate ramus of the pterygoid (QRPT) and the lateral lamina of the prootic (PROF) meet the medial surface of the quadrate (Figs 1, 19C, 26).

The quadrate is hollowed medially as in tritylodontids (Hopson 1966) and, as in these forms, is not buttressed firmly against the squamosal, although it still has no contact with the otic elements other than its medial contact with the lateral lamina of the prootic (see Figs 19C, 29A).

Quadratojugal (Figs 1, 19B, C, 25A, 26, 29A, B)

The present investigation has served to elucidate some features of this bone previously remarked on by Olson (1944) and Parrington (1946). The ventral end of the quadratojugal projects below the ventral border of the squamosal (Fig. 25A, SQ, QJ) but not sufficiently far down to make contact with the postdentary bones of the lower jaw normally. Contact may, however, have been established between the outer surfaces of the surangular and quadratojugal when the jaw was opened very widely (Fig. 25A, SAN). The upper part of the quadratojugal (Figs 1, 25A, QJFL) is expanded into a head, the dorsal surface of which is grooved (Fig. 26, GHQJ; Fig. 29B, QJ). The foot of the quadratojugal rests against the lateral surface of the quadrate at the base of the central thickening immediately above the lateral part of the condyle (Figs 25A, 26). The median surface of the vertical sheet of the quadratojugal (QJFL) and the lateral surface of the quadrate flange (QFL) are concave (Fig. 26). An anteriorly directed flange of the squamosal (Figs 1, 24C, 25A, 29A, SQS), which separates the quadrate and quadratojugal flanges, lies in this space between the concave surfaces of the two bones. A similar relationship is found in the cynognathids. The ventral surface of the foot of the quadratojugal is convex and fits into a concave quadrate surface (Figs 19B, 25A, 26, QJ, Q). The foot itself expands lateral to the vertical flange of the quadratojugal and the ventro-lateral part of the quadrate (Figs 1, 25A, 26). The lateral face of the quadratojugal flange is also concave, and another flange of the squamosal, expanded at its base, fits into the upper end of this concavity and helps to hold the quadratojugal in place (see e.g. Figs 1, 6B, 25A, 26).

Squamosal (Figs 1, 6B, 18A–20, 24C, 25A, 26, 29)

The present investigation added little to our knowledge of the squamosal. The pocket for the dorsal flange of the quadrate in the anterior face of the squamosal (Fig. 26, DQ) is only 1.6 mm deep. Another pocket (Fig. 26, DHQJ)

lies immediately lateral to the first and housed the grooved head of the quadratojugal (GHQJ). The anterior part of this pocket is confluent with that for the quadrate, but the posterior deeper part is initially separated from it by a thin wall of bone which expands posteriorly into the hind wall of the recess of the quadrate. The total depth of the pocket is 3,4 mm (Fig. 29B, QJ). Its posterior lower end is confluent with the deep notch for the quadratojugal flange in the posterior lower border of the squamosal. In anterior view the quadratojugal extends obliquely inwards and upwards into the pocket (see Fig. 26).

The tips of the quadrate ramus of the pterygoid (QRPT) and the lateral lamina of the prootic (PROF) reach the quadrate just in front of the inner wall of the pocket for the quadrate (Fig. 26). Crompton (1958: 191) has stated in error that in *Thrinaxodon* the quadrate ramus of the pterygoid does not reach the quadrate. In primitive cynodonts the quadrate rami of both the pterygoid and the epipterygoid reach the quadrate. The advanced cynognathids no longer retain the contact between the quadrate ramus of the pterygoid and the quadrate. *Cynognathus* does retain a contact between the epipterygoid and the quadrate. *Cynidiognathus*, which survived into Molteno Sandstone times (base of Stormberg Series overlying Beaufort Series), lacks this contact. Apparently the quadrate ramus of the pterygoid was withdrawn in early cynodonts and the quadrate ramus of the epipterygoid in late cynodonts.

Because the anterior surface of the paroccipital process is hollowed out, the antero-distal part appears as a distinct forward extension. This extension abuts against that part of the squamosal which forms the medial wall of the pocket for the quadrate (Figs 26, 29A, POPA). Because the distal surface of the paroccipital process does not make close contact with the squamosal (see e.g. Figs 26, 29B, POP, SQ), it seems reasonable to assume that the distal surface was covered by cartilage. Preservation of the distal end of the paroccipital process in *Cynidiognathus* (and possibly other cynognathids) also gives the impression that a cartilage cap may have been present. Such an arrangement might have been necessitated by some cranial kinetic movement at this point.

A distinct flange of the squamosal overhangs the posttemporal fossa (Fig. 2, PTF, SQ). This flange prevented constriction by the temporalis muscle of the veins (see above, Prootic, p. 373) which passed through the posttemporal fossa.

Orbitosphenoid

No trace of an orbitosphenoid was found in *Thrinaxodon*, but such an element was found in *Cynognathus* and *Cynidiognathus*, and has been described by Brink (1955a) in *Diademodon*.

Nasal septum and interorbital system

The presence during life of a nasal septum and an interorbital septum can be inferred from the structure of the vomer, the pterygoid and the parasphenoid. A groove runs along the median dorsal margins of the vomer and the para-

sphenoid (Fig. 6A, GR and all appropriate figures of sections). It seems probable that a nasal septum rested on the vertical plate of the vomer, a cribiform plate on the anterior part of the roof of the nasopharyngeal passage formed by the horizontal plate of the vomer, the palatine and the pterygoid, and an interorbital septum on the rostrum of the parasphenoid. No trace of an ossified interorbital septum similar to that found in *Cynognathus*, *Cynidiognathus*, and *Diademodon* was found. In these forms the median ossification is referred to as a presphenoid.

The existence of a cartilaginous posterior wall to the nasal capsule was suggested by Crompton (1958) for *Diarthrognathus* due to a difference in the matrix filling of the region where this structure would be expected. He suggested that such a difference in the matrix could be caused by finely suspended material which permeated through the more coarse material anterior and posterior to the space left by the disintegration of the cartilaginous wall. Possible evidence of a similar process was found in the sectioned skull of *Thrinaxodon*. The matrix in the nasal cavity itself is the same as that filling other cranial cavities and that surrounding the skull. In the left side of the snout a matrix which resembles fine quartz or calcite fills the space stretching from behind the posterior palatal foramina up to the choanae. This type of matrix differs conspicuously from the matrix found elsewhere in the skull.

Comparison with a model built of a sectioned skull of *Erinaceus europaeus* in the course of the present investigation shows that the position of this calcite-like matrix plate between the posterior palatal foramina and the choanae agrees exactly with the position occupied by a cribiform plate in a mammal. The problem is, however, that in mammals the secondary palate is more extensive posteriorly, so that the choanae are further back than in cynodonts. If the cribiform plate was indeed situated here in cynodonts there would apparently have been a gap between the posterior region of this plate and the interorbital septum further back. As this appears unlikely, the calcite-like filling should probably not be considered as an indication of a cribiform plate, or else its position is not a precise indication of the position occupied by the structure, the presence of which caused the calcite-like filling to develop. The presence of the calcite on the left side only may be a result of differences in the rate of disintegration of the possible cartilage.

Inner surface of the snout

A series of grooves and ridges on the inner surfaces of the nasals and frontals (Fig. 30A) is identical to those described by Watson (1913a) in *Nyctosaurus* and *Diademodon*. He considered these ridges and grooves, which closely resemble those in mammals, to be associated with the attachment of ethmoturbinals. On the inner surfaces of the maxillaries, similar but less pronounced ridges are found. These ridges may denote the presence of rudimentary maxilloturbinals. Similar grooves and ridges were also found in the cynognathids. Because this feature is generally associated with homoiothermy it is interesting

to find it even in early cynodonts, where the possibility of incipient homiothermy therefore must be considered.

Internal ear (Figs 27–29C)

The description given by Olson (1944: 28–29) of the internal ear of *Thrinaxodon liorhinus* is confirmed by the present study. The sacculo-cochlear recess (Figs 27A–29B, COE, CO, SR) is fairly big and ovoid in shape. The fenestra ovalis is situated lateral to it. The recess lies on the same level as the floor of the braincase. The major part of the outer border of the fenestra ovalis is formed by the prootic, its posterior and part of its inner border by the opisthotic, and the anterior inner part of its border by the basioccipital, which also forms part of the medial border of the sacculo-cochlear recess. A thick bony wall of the opisthotic (Fig. 28, ORSUSR) demarcates the sacculo-cochlear recess from the utriculus. The separation of the sacculo-cochlear recess and the jugular foramen by a ridge of the opisthotic (Fig. 28, ORSCRFJ) is incomplete. The ampullar recesses (AAMP, HAMP, PAMP) and the courses of the semicircular canals (Figs 28, 29, AVC, HC, PVC) are described accurately by Olson (1944) and Estes (1961).

The channel identified by Estes as a fenestra rotunda, which joins the fenestra ovalis and the jugular foramen, is very distinct in the *Thrinaxodon* skull reconstructed from serial sections in the present investigation (Figs 25A, FNA, 27B). A reconstruction of the inner ear structures (Fig. 28) added little to the descriptions by Olson and Estes. (See also under Supraoccipital, p. 378.)

(b) LOWER JAW (Figs 2, 31–33)

New information obtained by serial grinding of a very well-preserved skull and lower jaw and reconstruction on an enlarged scale makes it necessary to reconsider some features described and discussed by previous authors. These new features pertain mainly to the angular, articular and dentary.

Angular (Figs 14, 15, 17A–19B, 20, 22B, 25A, 31C, D, 32)

The reflected lamina (ANRFL) of the angular is preserved on the left side (Figs 17C, 31C, D, 32B). Here it is crescent-shaped, but broad as figured by Olson (1944). On the right side it is broken off, but it is likely that a slender, curved piece of bone found in the matrix on the medial side of the right ramus is actually the lamina. Parrington (1946) described the structure as a broad sheet of bone. He suggests that the anterior and lower parts, being more substantial than the rest of the structure, tend to remain in specimens in which the delicate sheet has been lost by weathering or preparation. Comparison with other specimens in the National Museum, Bloemfontein, in which the reflected lamina is preserved, indicates that the loss of the thin sheet, as Parrington suggests usually happens, would give the structure a crescent shape.

Parrington's (1955) investigations led him to conclude that the masseter in

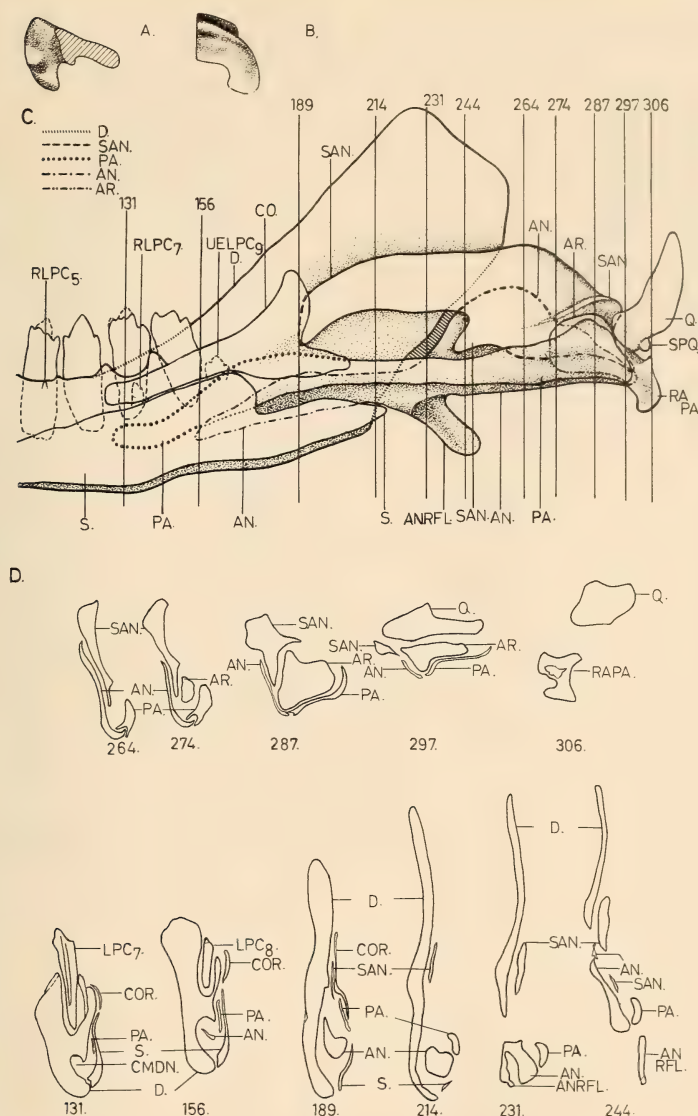


Fig. 31. A-B. Graphic reconstructions of anterior and medial views respectively of retroarticular process of articular on right side of serially sectioned skulls. C. Graphic reconstruction of posterior part of lower jaw in medial view to show form, position and relationships of comprising elements. Important levels to show how dentary and postdentary bones are joined together are indicated by the numbers of the sections of the serially sectioned skull and lower jaw. D. Sections indicated in C. $\times 2$.

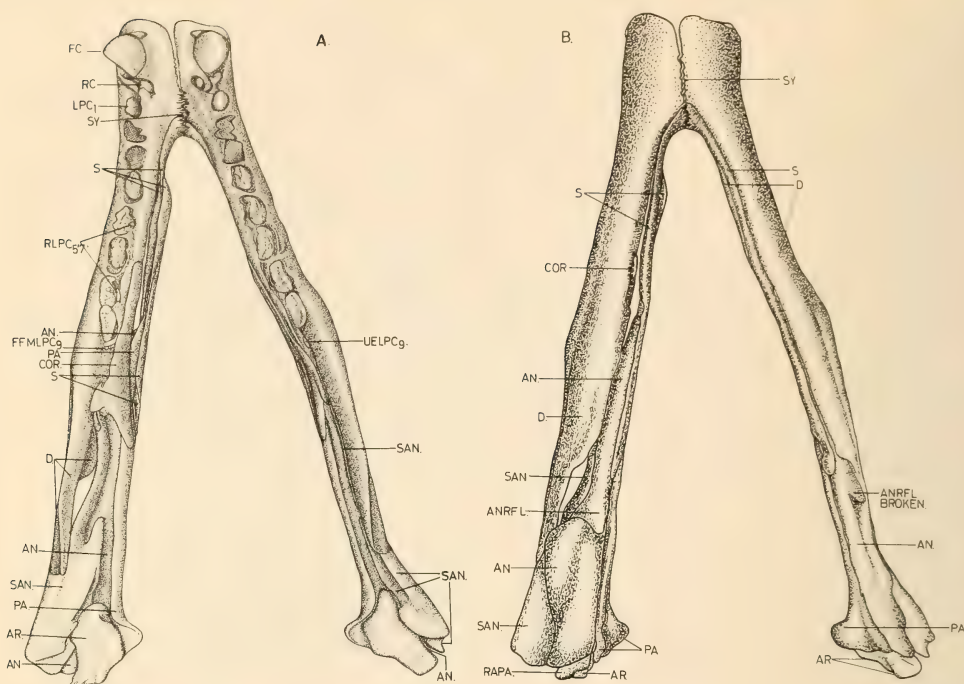


Fig. 32. Graphic reconstructions of lower jaw. A. Dorsal view; B. Ventral view. The latter is shown as a mirror image. $\times 1.5$.

gorgonopsids and in early cynodonts, like *Thrinaxodon*, was still inserted on to the reflected lamina of the angular. He suggested that the transfer of the insertion on to the dentary itself took place only in the advanced cynodonts with a large dentary. He believed that only then could the final reduction of the reflected lamina begin. Since the reflected lamina in *Thrinaxodon* is, however, already very much smaller than in *Gorgonopsia* and *Therocephalia*, and even slightly smaller than in procynosuchids, it appears probable that at least a large part of the masseter muscle must already have shifted its insertion on to the angle of the dentary. The very small reflected lamina figured by Broili & Schröder (1934a, 1935a) for *Cynognathus*, and the equally small one in *Trirachodon* specimens in the National Museum and in *Diademodon*, give the impression of it being a disappearing structure. It seems, therefore, that the reflected lamina had served

initially as insertion for the masseter muscle as Parrington (1955) concluded, but that it was already becoming unnecessary in the Middle Beaufort cynodonts where the masseter was already largely if not completely inserted on to the angle of the dentary.

Crompton (1963*b*) in his discussion of the origin of the mammalian lower jaw and its musculature accepted Parrington's suggestion that the masseter transferred from the reflected lamina on to the angle of the dentary. He suggested that there had been a superficial masseter inserting on the reflected lamina, and a deep masseter inserting on the postdentary bones. Migration of these muscles on to the dentary would have caused the reduction of the elements on to which they inserted.

Barghusen (1968) rejects these interpretations. On the basis of modern reptiles he believes that three muscles may originally have attached to the angular keel and massive reflected lamina in sphenacodonts and early therapsids. Of these three muscles he considers the branchiomandibularis as the most likely to have retained its attachment to the reflected lamina in cynodonts after the possible earlier pterygoideus musculature had been lost and the intermandibularis had shifted entirely on to the enlarged dentary, causing the reduction of the reflected lamina. He also concluded that the cynodonts indeed developed a masseter-like muscle, but in a manner different from that proposed by Parrington or Crompton. He believes that it differentiated from the external adductor and achieved insertion on the lateral surface of the dentary in primitive cynodonts. This insertion then migrated downwards to the postero-ventral edge of the dentary in later cynodonts. This development is uniquely cynodont and closely approaches the adductor jaw musculature of mammals. This is one of the reasons why cynodonts appear better fitted than any other group as the ancestors for all mammals.

Articular (Figs 19, 20, 31, 32)

The articular (AR) is held closely between the posterior lower half of the surangular (SAN) and the posterior part of the prearticular (PA) medially (Figs 31C, D_{274, 287, 297, 32}). It is a short solid bone with a pronounced bulge (Fig. 32A) towards the prearticular. Its median-dorsal surface is concave (Fig. 31D₂₈₇), a feature which is more pronounced along the central part of the bone than along its posterior part.

This concave median-dorsal surface results in a latero-dorsal ridge (Fig. 31B, D₂₈₇), which is made more pronounced because the vertical diameter of the bone is larger along the lateral margin of the bone than along the medial bulge. This bulge becomes progressively less distinct towards the posterior end of the bone, where it ends as a ridge on the upper medial surface of the retro-articular process (RAPA) (Fig. 31B, D_{297, 306}). Another ridge only becomes perceptible behind the central part of the bone. It runs backwards from the ventro-lateral surface (where it originates as a result of the medially directed bulge) to a ventro-median position, becoming progressively more distinct on

its way. Finally it terminates in the retroarticular process which is deflected downwards and forwards (Figs 31A, D_{287, 297, 306, 32B}).

The presence of a well-developed retroarticular process in *Thrinaxodon* has apparently not been described previously. Such a process is preserved only on the right articular of the serially ground skull (Figs 31A, B, C, D_{306, 32B}, RAPA) and is missing in all the other *Thrinaxodon* skulls in the National Museum. Apparently the retroarticular process in *Thrinaxodon* is particularly apt to break off either prior to fossilization or later during exposure and weathering.

Parrington (1955) discusses the mechanics of retroarticular processes. He examines the deflected articular process found in synapsids generally, and concludes that this deflected process is a true retroarticular process which gave attachment to a depressor mandibuli muscle in all the synapsids. This conclusion contradicts that of Watson (1948, 1951) who believes that in late synapsids the true retroarticular process had for the most part disappeared, and with it the depressor mandibuli muscle. According to Watson the posterior pterygoid muscle attached to the structure, which Parrington calls a retroarticular process in the late synapsids, and sublingual muscles (or muscles comparable with those of mammals) opened the jaw. Parrington shows that the functional implications of this determination raises grounds for doubting Watson's interpretations. An interpretation of the disputed structure and its modifications as a retroarticular process allows for a straightforward explanation in terms of jaw-mechanics.

Dentary and splenial (Figs 2-4, 8, 9, 11, 14, 15, 17A-18B, 22B, 31C, D, 32)

Each lower jaw ramus is formed mainly by the dentary which is joined by an interdigitated suture only at its extreme anterior end to the dentary of the opposite ramus (Fig. 32, SY). The posterior part of the lower jaw symphysis is formed by an interdigitated suture between the two opposite splenials (Fig. 32, S). The anterior part of the splenial which takes part in the symphysis, is thick and solid (Fig. 8A, S) compared with the rest of the bone which has a thin upper and somewhat thicker lower part (Figs 9, 11, 14, S). The splenial lies against the lower half of the medial surface of the dentary where the expanded lower end of the splenial fits into an excavation along the lower part of the dentary.

Due to the loss of the incisor bearing part of the mandible, the mandibular canal (Figs 8-10, CMDN) for the ramus mandibularis of the trigeminal nerve could not be traced further forward than the canine alveolus into the base of which it enters. The major part of the canal anterior to the seventh postcanine lies entirely in the dentary. It runs just below the bases of the postcanine alveoli, with each of which it retains contact. Behind the seventh alveolus the medial wall of the canal is formed by the splenial. The anterior end of the prearticular, which is inserted between the medial surface of the dentary and the upper part of the splenial, extends forward to this level where the mandibular canal enters the dentary (Figs 11B, 31C, D_{131, 32, PA}). The tip of the prearticular lies just above

the mandibular canal. This bone, which is very thin, is expanded dorso-ventrally for some distance behind the level of the eighth lower postcanine (Fig. 31C, PA). Its lower end reaches down below the upper medial dentary margin of the mandibular canal. Thus it forms the upper part of the medial wall of the posterior part of this canal into which the anterior end of the angular penetrates as far as the eighth postcanine (Fig. 31C, D₁₅₆, AN). Above the mandibular canal behind the seventh postcanine, the medial surface of the dentary is slightly concave, apparently to aid in the attachment to the dentary of the prearticular and splenial, and further back the coronoid (Figs 14-15B, D, S, PA, COR). The channel in the dentary behind the seventh postcanine becomes progressively higher. The medial part of its upper wall is formed by the lower surface of the tooth-bearing ridge (Figs 11B, 14A, B). Where this structure ends well behind the anterior border of the coronoid process of the dentary, a medio-ventrally directed ledge forms the upper wall of the channel for approximately a further 5 mm. Behind this ledge there is no further indication of the mandibular canal.

The anterior end of the angular which penetrates into the mandibular canal divides it into an upper and a lower half. Along the dorsal surface of the angular runs a groove of which the lateral wall is considerably higher than the medial one. This groove extends as far back as the angle of the dentary (Figs 14, 15, D, AN). Still further back the reflected lamina (ANRFL) is attached to the base (Fig. 17B, C) of the angular and immediately behind this level the angular is considerably expanded in a dorsal direction (Figs 31C, D₂₄₄, AN). This part of the bone is tilted laterally, with its dorsal margin directly below the lower margin of the coronoid process of the dentary. This part of the angular has a peculiarly contoured shape to maintain a close relationship between itself, the prearticular and the surangular. This latter bone lies against the inner surface of the upper half of the angular which is curved in such a way as to form a ledge for the support of the surangular, the posterior half of which is expanded in a ventral direction (Figs 31C, D_{264, 274}, 32A, AN, SAN). The lower margin of the posterior half of the angular is curved medio-dorsally and fits into a groove along the ventral surface of the posterior part of the prearticular (Figs 31D_{264, 274, 287}, 32B, PA) thus forming a schindylesis or wedge-and-groove suture. Anterior to the reflected lamina of the angular, the prearticular lies at the medio-dorsal margin of the angular. Because the lateral surface of the prearticular is concave, a channel is formed between the concave dorsal surface of the angular and the concave lateral surface of the prearticular (Figs 31D₁₅₆₋₂₇₄, 32A, AN, PA).

The articular inserts into the posterior part of this channel (Figs 31D_{274, 287, 297}, 32A, AR). Its anterior dorsal surface is concave (grooved) and covered laterally by a peculiar ledge of the surangular (Figs 31C, D_{274, 287}, 32A, SAN).

A possible course for the ramus mandibularis of the trigeminal can now be suggested. It probably ran backwards in the mandibular canal; then along the dorsal surface of the angular where the latter penetrates into the canal; then along the channel formed by the dorsal and further back the medio-dorsal

surface of the angular and the lateral surface of the prearticular; then along the dorsal surface of the anterior part of the articular which inserts into the angular-prearticular channel. From the articular, but in front of the quadrate, the ramus mandibularis probably passed sharply medianly and dorsally in front of the stapes. At its base the lateral lamina of the prootic is notched on its anterior margin. Passing through this notch the ramus mandibularis then probably entered into the cranial cavity via the large foramen between the prootic and epipterygoid.

Coronoid (Figs 11B, 14A–15B, 31C, D, 32A)

The tip of the coronoid lies just behind the sixth postcanine. The bone extends along the medio-dorsal surface of the dentary above the splenial, prearticular and angular. In this region the upper part of the coronoid lies above the dorsal margin of that part of the dentary which forms the medial wall of the eighth postcanine alveolus. The ninth postcanine alveolus, which is partly formed, has a crown of an unerupted tooth of much smaller size than the eighth in it. The dentary has hardly any part in the formation of the medial wall of the ninth alveolus. The coronoid covers the partly formed ninth alveolus medially (Figs 14B, 31C, 32A, COR, UELPC₉). Behind this ninth alveolus the coronoid increases considerably in height (Figs 31C, 32A, COR). Its upper part is thicker than its lower edge which covers the upper edge of the prearticular (Figs 15A, B, 31C, COR, PA). The medial surface of the coronoid process of the dentary behind and above the postcanine alveoli is concave to receive the upper part of the coronoid (Figs 15A, B, 31D₁₈₉, D, COR). Just behind the tip of the surangular which is inserted between the coronoid and the dentary, the coronoid bifurcates into an upper part which ends abruptly and a lower part which extends backwards for about 3,5 mm along the upper part of the medial surface of the prearticular (Figs 31C, 32A, COR, PA).

Surangular (Figs 17A–19B, 20, 22B, 25A, 31C, D, 32)

The surangular has a long anterior portion. This part of the bone is very thin and lies in a shallow depression on the medial surface of the coronoid process of the dentary. On the lateral surface of this coronoid process is a ridge, the position of which (Fig. 31D_{214, 231, 244}, D, SAN) corresponds with the medial depression for the surangular. This ridge, which runs obliquely upwards towards the posterior margin of the dentary, forms the lower margin of the insertion area of the masseter muscle.

Towards and beyond the posterior margin of the coronoid process of the dentary the long anterior and the posterior parts of the surangular become progressively thicker. Well behind the coronoid process and above the reflected lamina of the angular, the surangular bears an antero-ventrally directed process, 2 mm long, below the long anterior part of the bone. The base of this process is that part of the bone which is expanded in a ventral direction and lies medial to that part of the angular which is expanded in a dorsal direction (Figs 31C,

32A, SAN, AN). The relationships of the angular and surangular have been described above (see p. 389).

Some reference has been made to the relationship between the surangular and the articular (see p. 387). The lower edge of the surangular lies against the lateral surface of the articular. Less than 2 mm anterior to, but above the tip of the articular, a ridge begins on the medial surface of the surangular (Figs 31C, 32A, AR, SAN). Further back this ridge progressively expands into a ledge running above the lateral part of the articular. The upper half of the surangular, which has a concave medial face and a thickened dorsal edge, ends on the ledge (Figs 31C, D_{264, 274, 287}, 32A, SAN). The ledge itself ends just behind the bulky anterior part of the articular, and the thin lower edge of the bone ends along the flattened neck about half-way between the anterior part of the articular and the retroarticular process (Figs 31C, D₂₉₇, 32A, AR, SAN, RAPA).

Prearticular (Figs 11B, 14A–15C, 17A–19B, 20, 22B, 25A, 31C, D, 32)

The relationships of the prearticular with the dentary and splenial (see p. 388) and with the angular (see p. 389) have been described above. It can also be noted that the posterior part of the prearticular, of which the ventral margin is grooved for insertion of the medio-dorsally curved ventral margin of the angular, is increasingly tilted medially further back where it is a broad thin plate. This structure is correlated with the rapid progressive increase in diameter of the anterior part of the articular of which the medial surface is covered by the prearticular which closely follows its contours (Figs 31D_{287, 297}, 32A, AR, PA). Only between the postero-dorsal part of the medial face of the articular, and the postero-dorsal part of the lateral face of the prearticular is there an interspace which may be an indication of the presence of the tensor tympani muscle (Fig. 31D₂₉₇). In mammals this muscle is typically inserted on to the medial surface of the malleus, which is considered homologous with the articular and runs forward to its origin on the base of the skull.

(c) DENTITION (Figs 1, 3–11B, 13B₂–14B, 31C, D, 32A, 33)

A detailed description of the dentition of *Thrinaxodon liorhinus* is deemed unnecessary because of the work done by Crompton and co-workers in recent years. However, since they limited their studies to the postcanines, a few points of interest about the incisors and canines revealed by the study on which this paper is based may be mentioned.

Specimens actually investigated by the present author or described in the literature reveal evidence of at least four replacements of the incisors between the 35 mm and the 88 mm skull-length stages. Crompton (1955c) has pointed out that in the cynodonts investigated by him replacement of incisors and canines is found much more frequently than replacement of postcanines. This phenomenon is due, he believes, to the fact that incisors and canines form an arc whereas postcanines form a linear series. During growth those parts of the

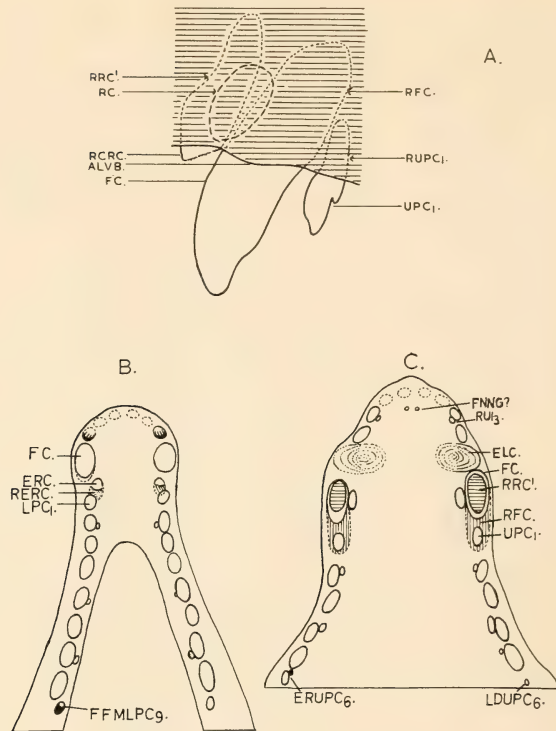


Fig. 33. A. Graphic reconstruction to show relative positions of replaced, functional and replacing upper canines. B-C. Graphic reconstructions of lower and upper dentitions. Only outlines of teeth crowns are shown and replacing postcanines are shown in their true position with respect to the functional teeth. Lost incisors are indicated by dotted outlines only. Alveoli of lost replacing teeth are shown in black.

A $\times 2.5$. B-C $\times 1.25$.

mandible and upper jaw containing incisors and canines increase greatly in size. Frequent replacement of the functional teeth by larger ones would, therefore, ensure that functional teeth occupied the entire region.

The current investigation of *Thrinaxodon* and the later cynodonts shows that the type of replacement of the canines in these forms is identical with that found by Kermack (1956) in the therocephalians and gorgonopsians which he investigated. Although the crowns of the canines are apparently shed, the roots are retained (Figs 3, 33A, (R)RC¹) and are gradually resorbed, thus apparently aiding the calcium (and phosphate?) metabolism of the animal. There is some evidence that the alternation of consecutive generations of functional canines between the anterior and posterior halves of the alveolus, observed by Kermack, can also take place in *Thrinaxodon*. One example of an upper replacing canine

erupting posterolingual to the functional one was found. In all other specimens investigated the replacing canine was anterolingual to the functional one. Evidence of the bone plug which closes the unoccupied part of the alveolus until the new canine erupts, was found in the lower canine alveoli of the sectioned skull (Fig. 3A, BP). Consideration of all available evidence suggests at least six and probably seven or more replacements of the functional canines.

SUMMARY

1. A skull of *Thrinaxodon liorhinus* has been serially sectioned at intervals of 200μ , and an enlarged wax model built. New details on the structure of the component bones of the skull and their relationships are described and figured. The processes of the premaxillary and their contacts with the maxillary are described and figured. The canals in the maxillary are described and functional and replacement teeth are indicated. The canals in the lacrimal and the relationships of this bone with the maxillary and palatine to form the maxillary antrum are indicated. Grooves and ridges on the inner surface of the roof of the snout, possibly for the attachment of turbinals, are figured.

The vomer with a groove along its dorsal margin is described and it is shown that the double anterior end suggests a paired origin of the bone. The relationships of the premaxillary with the lower end of the vomer are indicated as well as a possible explanation for the thickened lower margin of the anterior vertical part of the bone and the medial dorsal margins of the maxillaries. An explanation is also offered for the ridges on the ventral surface of the palatine and pterygoid. The exact relationship of the posterior parts of the pterygoids and the parasphenoid rostrum is indicated. It is shown that interdigitated sutures preclude the possibility of kinetic movement in this region. It is suggested that the groove dorsally along the vomer, and on the dorsal surface of the parasphenoid rostrum, may indicate the presence of a cartilaginous nasal septum and an interorbital septum. Evidence in the matrix of a possible cartilaginous cribriform plate at the posterior end of the snout is described. The relationship of the anterior ventral part of the epipterygoid and the pterygoid is indicated as well as that of the epipterygoid and prootic. The walls of the braincase are described in detail, externally and internally. The interpretations of Watson and Cox of the venous system on the walls of the braincase in cynodonts and anomodonts are compared with conditions in *Thrinaxodon* and an interpretation of the condition in this form is suggested.

The structures of the prootic and opisthotic to accommodate the internal ear structures are described and figured. The presence of a possible fenestra rotunda is confirmed. The exact way in which the abducent foramen is formed is described. The possible courses of the maxillary, mandibular and deep ophthalmic rami of the trigeminal, the abducent and the palatine ramus of the facial nerves are described. A possible Eustachian foramen is indicated as well as a possible separate foramen for the internal jugular vein. The basicranial region is described and it is shown that the sella turcica is very shallow and that there

is hardly any dorsum sellae. The stapes is described in detail and it is shown that it has three processes on its distal end; these are a dorsal process towards the paroccipital, a quadrate process, and, as preserved, a minute process towards the base of the external auditory meatus. The relationships of the quadrate and quadratojugal with each other as described by Parrington (1946) are confirmed and their relationships with the squamosal are described. Parrington's (1946) description of a canal penetrating the quadrate is confirmed. A stapelial process on the quadrate is described. The elements of the lower jaw are described in detail and their relationships with each other are figured in different views. A retroarticular process is described for the articular.

2. It is shown that the incisors are replaced at least four times and that during replacement the crown of the functional canine is shed, but that the root is gradually resorbed. Only one example of an upper replacing canine erupting postero-lingual to the functional one was found. In all other specimens investigated the erupting replacing canine was in the antero-lingual position in relation to the functional canine. More definite evidence of the alternation of the functional canine between the anterior and posterior halves of the alveolus seems to be needed.

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KEY TO LETTERING

AAMP	anterior ampulla
ADP	antero-dorsal process of the prootic
AN	angular
ANRFL	reflected lamina of the angular
AR	articular
ARCA	attachment of the rectus capitis anticus muscle
AVC	anterior vertical semicircular canal
AWELC	premaxillary part of the anterior wall of the excavation for the lower canine
BCP	basicranial process
BO	basioccipital
BP	bone plug
BPTP	basipterygoid process of the basisphenoid
BPTPL	basal plate of the epipterygoid resting on the basipterygoid process
BQREPT	broken quadrate ramus of the epipterygoid
BSCROPPT	continuation on to the basisphenoid of the ridge formed by the outer prong of the pterygoid.
BS	basisphenoid
BSY	broken symphysis
CC	crus communis
CCA	carotid canal
CEPT	cavum epitericum
CH	choanae
CMDN	canal for the mandibular nerve
CMN	canal for the maxillary nerve
CO	cochlea
COE	cochlear extension
COR	coronoid
CPD	damaged coronoid process of the dentary
CPR _{vii}	canal for the palatine ramus of the facial nerve
CRMAX _v	probable course of the maxillary ramus of the trigeminal nerve
CROP _v	probable course of the ramus ophthalmicus profundus of the trigeminal nerve
CRPAL _{vii}	probable course of the palatine ramus of the facial nerve
CV	vena communicans between vena capitis dorsalis and vena capitis lateralis
D	dentary
DF	displaced fragment
DFPT	displaced fragment of the transverse flange of the pterygoid
DG	depression for a gland
DHQJ	depression on the squamosal for the head of the quadratojugal
DLBMN	duct for the lacrimal branch of the maxillary nerve
DORS	dorsal
DPS	dorsal process of the stapes
DQ	depression for the quadrate on the squamosal
DRUPC ₂	displaced second replacing upper postcanine
DT	displaced tooth
DTCMN	double termination of the canal for the maxillary branch of the trigeminal nerve
DV	double anterior end of the vomer
EAM	external auditory meatus
EDLBMN	entrance of the duct for the lacrimal branch of the maxillary ramus of the trigeminal nerve
EIMC	entrance of the independent maxillary canal
ELC	excavation for the canine of the lower jaw
ELD	entrance into lacrimal duct
EPT	epipterygoid
EPTR	ectopterygoid
ERC	erupting replacing canine
ERUPC ₂	erupting replacing second upper postcanine
ES	extrastapes

EUPC	erupting upper postcanine
EXO	exoccipital
FC	functional canine
FDTCMN	foramina of double termination of canal for the maxillary ramus of the trigeminal nerve
FEPTR	foramen in the ectopterygoid
F _v	foramen for trigeminal nerve
F _{vi}	foramen for abducent nerve
F _{vii}	foramen for facial nerve
F _{xii}	foramen for hypoglossal nerve
F	frontal
FFMLPC ₉	displaced main fragment of the developing ninth lower postcanine
FIMC	foramen of the independent maxillary canal
FIN	foramen incisivum
FJ	foramen jugulare
FLA	foramen lacerum anterium
FLBMN	foramen for the lacrimal branch of the maxillary ramus of the trigeminal nerve
FM	foramen magnum
FN ₁	foramen for Eustachian tube (?)
FN ₂	foramen for internal jugular vein (?)
FNA	fenestra rotunda
FNNG	foramen of canal to Organ of Jacobson and nasal gland
FO	fenestra ovalis
FPOP	fragment of the paroccipital process
FPT	foramen pterygoideum
FRAC	fracture
FSA	fossa subarcuata
FSC	foramen for the vena capitis dorsalis in the sinus canal
GDV	groove along the dorsal margin of the vertical plate of the vomer
GHQJ	grooved head of the quadratojugal
GR	groove
GRPR _{vii}	groove for the palatine ramus of the facial nerve
GRVSC	groove for the vein of the sinus canal
HAMP	ampulla for the horizontal semicircular canal
ICF	internal carotid foramen.
IDIOPPT	excavation on pterygoid beyond which the inner and outer prongs separate
IMC	independent maxillary canal
INPPX	internarial process of the premaxillary
IPAR	interparietal
IPPT	inner prong of the pterygoid
J	jugal
KVP	keeled vomer plate
KVPG	keeled vomer plate with groove
L	lacrimal
LD	lacrimal duct
LDUPC	remnant of the lost developing sixth upper postcanine
LEX	lingual excavation
LF	lacrimal foramen
LLCL	recess for the lateral lobe of the cerebellum
LLF _{xii}	large lower foramen of the hypoglossal nerve
LPC _x	lower postcanine number x
LRC	replacing lower canine
MAN	maxillary antrum
MP	mastoid process
MPPX	maxillary process of the premaxillary
MX	maxillary
MXPS	maxillary-palatine suture
N	nasal
NO	nostril

O	orbit
OPO	opisthotic
OPPT	outer prong of the pterygoid
ORSCRFJ	opisthotic ridge separating the cochlear recess and the jugular foramen
ORSUSR	opisthotic ridge separating utricular and saccular recesses
P	palatine
PA	prearticular
PAMP	posterior ampulla
PAO	pila antotica
PAR	parietal
PCP	cultriform process (= rostrum) of the parasphenoid
PF	parietal foramen
PITF	pituitary fossa
PO	postorbital
PODG	postdentary groove
POP	paroccipital process
POPA	paroccipital process abutting against the squamosal
POPARS	postorbital-parietal suture
PPF	posterior palatal foramen
PPLMX	palatal plate of the maxillary
PPPX	palatal process of the premaxillary
PPPXSP	short prong of the palatal process of the premaxillary
PPRASP	posterior palatine part of the ridge for the attachment of the soft palate
PRF	prefrontal
PRO	prootic
PROF	prootic flange
PRON	inner fork of the antero-dorsal process of the prootic
PS	parasphenoid
PS-BS	parasphenoid-basisphenoid
PT	pterygoid
PTF	posttemporal fossa
PTPOF	pterygo-paroccipital foramen
PTPRQ	pterygoid process of the quadrate
PTPSS	pterygoid-parasphenoid suture
PTRASP	pterygoid part of the ridge for the attachment of the soft palate
PVC	posterior vertical semicircular canal
PVCJUT	posterior vertical semicircular canal joins utriculus
PX	premaxillary
Q	quadrate
QC	quadrate canal
QFL	quadrate flange
QJ	quadratojugal
QJFL	quadratojugal flange
QJN	notch for the flange of the quadratojugal
QN	notch for the flange of the quadrate
QPS	quadrate process of the stapes
QREPT	quadrate ramus of the epipterygoid
QRPT	quadrate ramus of the pterygoid
RAMCP	ridge for the attachment of the mucous covering of the palate
RAPA	retroarticular process of the articular
RASP	ridge for the attachment of the soft palate
RC	replacing canine
RC ¹	root of the replaced canine
RCRC	remains of the crown of the replaced canine
RERC	root of the erupting replacing canine
RFC	root of the functional canine
RFMLPC ₉	remaining fragment of the 9th lower postcanine
RHC	rhinarial canal
RLPC _x	X-th replacing lower postcanine

ROLI ₃	root of the third lower incisor
ROVCL	root of the vena capitis lateralis
RRC ¹	root of the replaced canine
RUI ₃	replacing third upper incisor
RUPC _x	X-th replacing upper postcanine
SAC	sacculus
SAN	surangular
SC	sinus canal
SET	sella turcica
SF	stapedial foramen
SMX	septomaxillary
SPBPPPX	small process at the base of the palatal process of the premaxillary
SPQ	stapedial process of the quadrate
SPRO	spur of the prootic
SQ	squamosal
SQS	flange of the squamosal protruding forward between the quadrate and quadrato-jugal
SR	saccular recess
S	splénial
ST	stapes
STR	stapedial recess
SUOC	supraoccipital
SY	symphysis
TAB	tabular
TCP	thin coronoid process
TFPT	transverse flange of the pterygoid
UELPC ₉	ninth lower postcanine which had not yet erupted
UI ₃	third upper incisor
UPC _x	X-th upper postcanine
UPPPPX	upper prong of the palatal process of the premaxillary
UR	utricular recess
USW	unossified side wall of the braincase
UT	utricle
UZ	unossified zone
V	vomer
VCD	vena capitis dorsalis
VCL	vena capitis lateralis
VG	venous groove
VP	vomer plate
VPAR	vena parietalis
WPS	wing of the parasphenoid
WQRSQ	wall of the recess for the quadrate on the squamosal
WST	wall of the sella turcica

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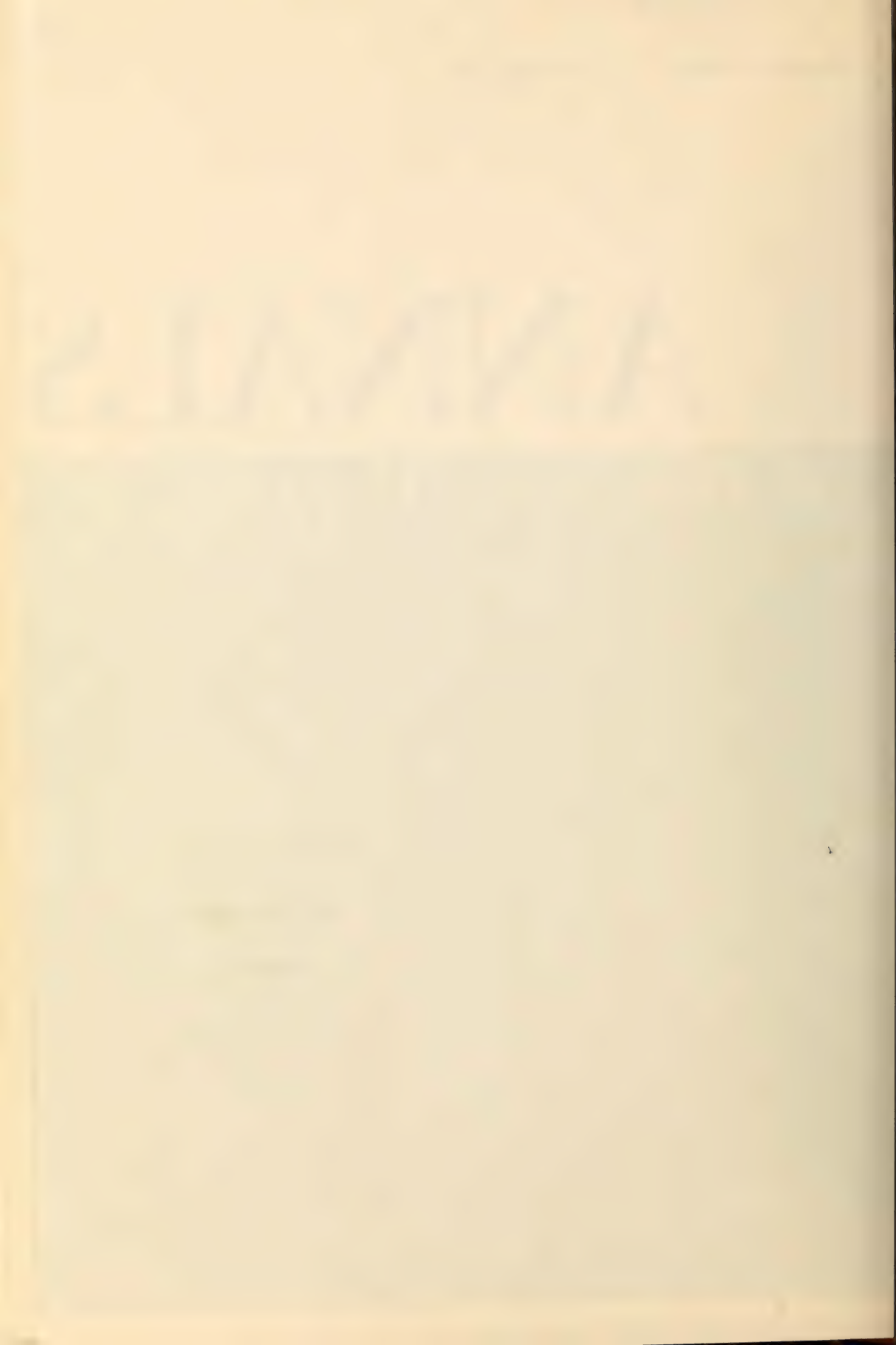
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By
BRIAN KENSLEY

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(With 30 figures and 18 tables)

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INTRODUCTION

The isopod genus *Tylos* Latreille belongs to the suborder Oniscoidea which includes a miscellany of more or less terrestrial forms. This group has been split into two series by Vandel (1943), viz. the Tylienne and the Ligienne. The former contains two families, the Tylidae and the Stenoniscidae, while the latter contains about 20 families, including all the true terrestrial isopods. After an exhaustive investigation into the anatomy and morphology of the Oniscoidea, Vandel (1943) came to the not surprising conclusion that this heterogeneous suborder has a polyphyletic origin. The Tylienne series, which is not truly terrestrial and contains mostly halophilic species which are still dependent on the marine environment, is derived from the marine Valvifera group, having many structural similarities. The Ligienne series is derived from some marine family, possibly the Cirolanidae. This group, which has occupied numerous terrestrial niches, shows almost perfect adaptation to terrestrial life.

This paper was submitted in 1970 in partial fulfilment of the requirements of the Degree of Master of Science in Zoology at the University of Stellenbosch.

The family Tylidæ contains the single genus *Tylos* Latreille comprising at present 15 known species, the distribution of which may be seen in the following list, adapted from Vandel (1945).

Southern Group	<i>capensis</i> Krauss	South Africa
	<i>granulatus</i> Krauss	South Africa
	<i>neozelanicus</i> Chilton	New Zealand
	<i>spinulosus</i> Dana	South America
	<i>wegeneri</i> Van Name	Venezuela
West Pacific Group	<i>granuliferus</i> Budde-Lund	Borneo & Japan
	<i>opercularis</i> Budde-Lund	Philippines
Indian Ocean Group	<i>albidus</i> Budde-Lund	Nicobar Island
	<i>minor</i> Dollfus	Seychelles
	<i>nudulus</i> Budde-Lund	Christmas Island
Red Sea Group	<i>exiguus</i> Stebbing	Red Sea (possibly synonymous with <i>latreillei</i>)
Northern Group	<i>insularis</i> Van Name	Galapagos Island
	<i>latreillei</i> Audouin	Mediterranean, North and Central America
	<i>niveus</i> Budde-Lund	Florida, Cuba, Venezuela
	<i>punctatus</i> Holmes & Gray	California, Mexico

The similarities of the species of the southern group has led Vandel to suggest a Gondwana origin for this group, in which he includes the Venezuelan *wegeneri* for its similarities to *capensis*.

Since 1843, when the German naturalist Krauss described *T. granulatus* and *T. capensis* from the Cape, many records of these species have been made. Most of these merely mention the animals' occurrence, or are brief morphological notes with a view to their easy identification. Barnard, in three separate papers (1925, 1934, 1940), has written the most about these species, and while his descriptions of the structure are excellent, it is felt that some of his ideas regarding the reproduction and digestion might require revision.

As both species, by virtue of their large numbers, form an important part of many sandy beach ecosystems of South Africa, it was felt that an ecological study would be particularly interesting and would reveal both the similarities and differences of the two species. This study was thus undertaken in an attempt to document and explain the many observations made. Simultaneously, the work on the European *T. latreillei* by Mead (1968), Matzakís (1956), Soika (1954), and Arcangeli (1953), was borne in mind, and the similarities and differences noted.

DESCRIPTION OF SPECIES

As a complete description of the external morphology of both species has not yet been published, this has been done as a preliminary to the ecological descriptions. A list as complete as possible of all references to the two species is included.

Tylos granulatus Krauss, 1843

Tylos granulatus Krauss, 1843: 64, pl. 4, fig. 5. Budde-Lund, 1885: 275; 1906: 74, pl. 3, figs 21–24; 1909: 70. Dollfus, 1895: 352. Stebbing, 1910: 43. Barnard, 1924: 236; 1925: 29, fig. 3; 1932: 217. Panning, 1924: 172. Vandel, 1945: 227; 1943: 40. Brown, 1959: 470.

Pleistocene fossil: Houghton, 1931: 27.

Body oval—elongate, widest at fifth or sixth segment. Integument chitinous, transparent, thick, covered with numerous flattened roughly elliptical granules (Fig. 4c). Membranous subintegumental layer bearing branched chromatophores. Head (Fig. 1) evenly convex, bearing two compound eyes dorso-

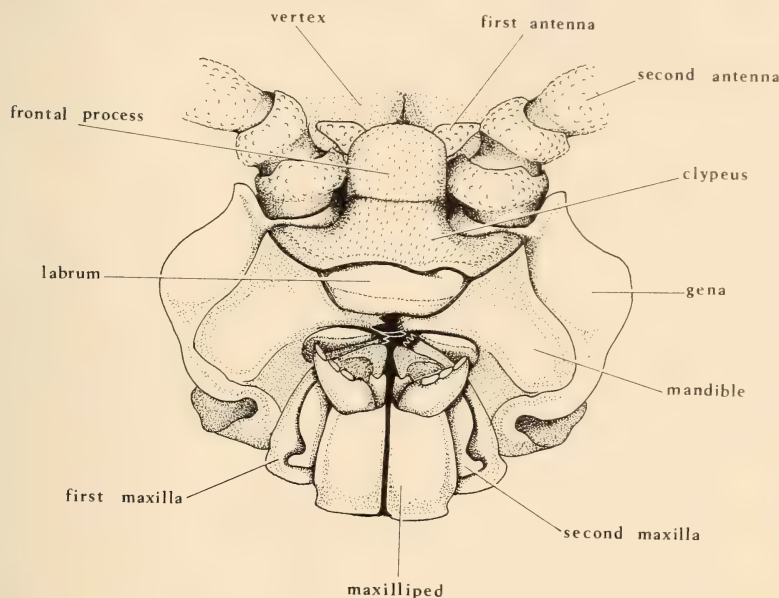


Fig. 1. *Tylos granulatus*. Anterior view of head.

laterally, each composed of about 50 ommatidia. No distinct frontal line, but faint impressed line joining anterior margins of eyes, becoming obsolete mid-dorsally. Vertex narrowed antero-ventrally between first antennae, giving way to broadly rounded frontal process. Broad clypeus below frontal process, with labrum ventrally attached. Labrum asymmetrical due to underlying left mandible atop right mandible. Narrow gena situated lateral to second antennae, ventrally embracing mandibular bases.

Head appendages—first antenna consisting of single almost immobile segment medio-dorsal to second antenna, dorsally flattened, triangular, level with rest of vertex, ventrally with broad articulating area, with socket-like depression near apex of triangle, containing numerous aesthetascs. Second antenna (Fig. 2c) stout, elongate, consisting of five basal segments plus flagellum

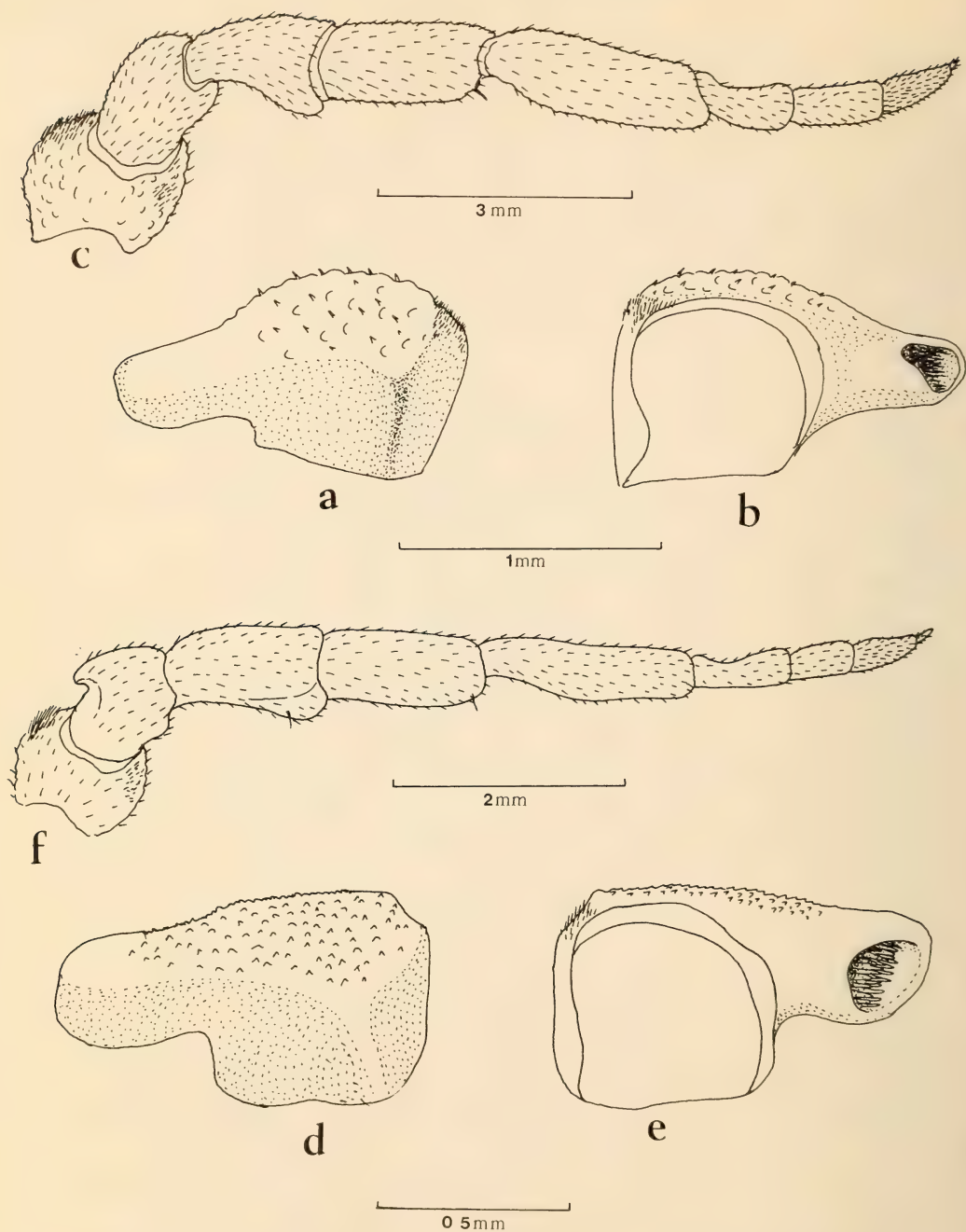


Fig. 2. a. *Tylos granulated*. External view of first antenna. b. Internal view of first antenna. c. Second antenna. d. *Tylos capensis*. External view of first antenna. e. Internal view of first antenna. f. Second antenna.

of four smaller segments, terminal segment minute. Surface granular, with numerous setae, especially on terminal and subterminal segments. Mandibles powerful, heavily chitinised. Left mandible (Fig. 3a) with incisor process of three powerful teeth. Lacinia mobilis also strongly chitinized with three teeth,

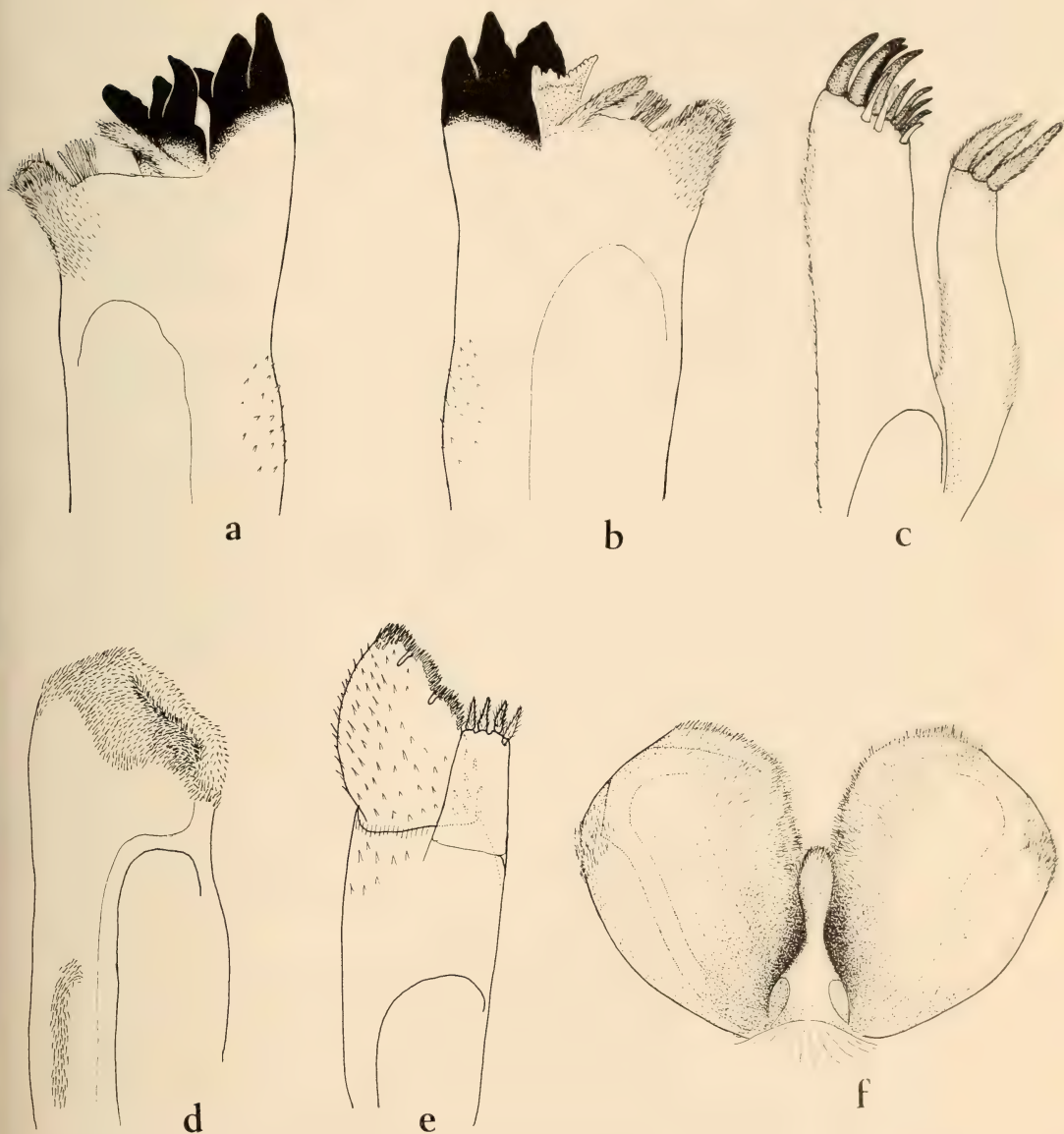


Fig. 3. *Tylos granulatus*. a. Left mandible. b. Right mandible. c. First maxilla. d. Second maxilla. e. Maxilliped. f. Labium.

with setose lobe at base. Latter followed by group of 10–12 penicillae, exterior to which, heavily setose molar process bearing terminal rasp-like process. Right mandible (Fig. 3b) similar to left, differing only in lacinia mobilis, which is very reduced, not heavily chitinized. Incisor process fits between lacinia mobilis and incisor process of left mandible. First maxilla (Fig. 3c) bilobed, consisting of two endites, outer lobe longer than inner, with setae along entire outer margin, bearing about 11 or 12 terminal hooked teeth of varying size, larger ones strongly chitinised. Inner lobe terminated with three stout setose penicillae. Second maxilla (Fig. 3d) consisting of single broad lamella, terminally heavily setose, bearing groove on inner face. Maxilliped (Fig. 3e) consisting of coxa, and basopodite bearing palp and endite. Broad strong palp with most of external surface armed with flattened blunt spines. Median edge divisible into three sections, reflecting fusion of three segments, each bearing numerous close-set blunt spines. Endite smaller than palp, terminated with five setose penicillae. Lobed lower lip (Fig. 3f) just ventral to mandibles, heavily setose on medio-dorsal surfaces. Tongue-like median setose lobe at base of outer lobes.

Pereion—consisting of seven segments, all except first having epimerites (Fig. 4a), those of segments six and seven being quadrate, large, those of other

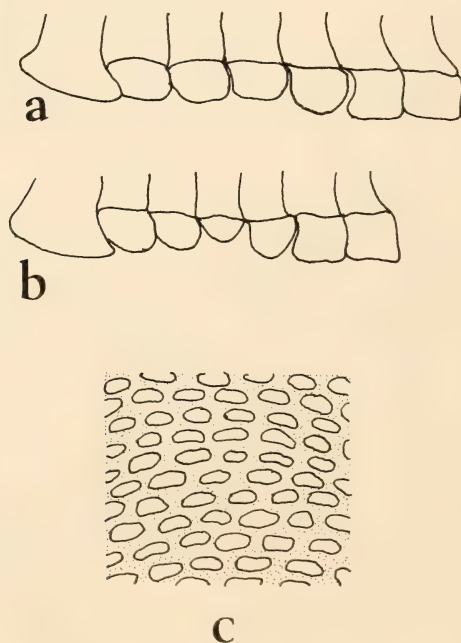


Fig. 4. a. *Tylos granulatus*. Pereion epimerites. b. *Tylos capensis*. Pereion epimerites. c. One square millimetre of exoskeleton surface, showing granulation.

segments being smaller, rectangular/triangular. Seven pairs of pereopods present, first four pairs being forwardly directed, differing slightly from three posteriorly directed pairs. Each pereopod consisting of six segments, basopodite largest. An obvious angle between basis and rest of leg. Anterior four pairs of pereopods (Fig. 5a) with basis equal to ischium + carpus + merus in length. Merus with large rounded dorsal lobe. Carpus, propodus, and dactylus together forming a claw. Numerous spines and setae present on all segments, especially on more terminal ones. Posterior three pairs of pereopods (Fig. 5b) with basis equal to ischium + merus in length. Dactylus small; propodus, carpus, and merus stout, with strong spination. In ovigerous females, lamellar oostegites present on all pereopods.

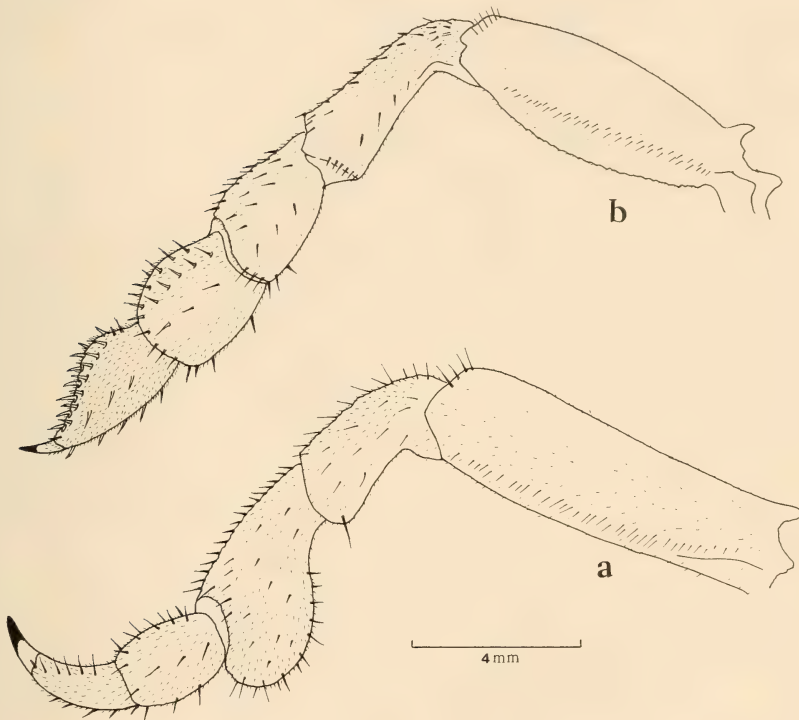


Fig. 5. *Tylos granulatus*. a. Second pereopod. b. Fifth pereopod.

Pleon—consisting of five free segments, plus rectangular telson. Latter twice broader than long. Five pairs pleopods present (Fig. 6), first pair reduced to slender lamella, posterior four pairs consisting of basis plus endo- and exopodite. Both latter lamellar, performing respiratory function. Exopod with numerous vertical folds, endopod with irregular folds. Second to fourth exopods with posterior pointed process medially. Endopod of second pleopod in male

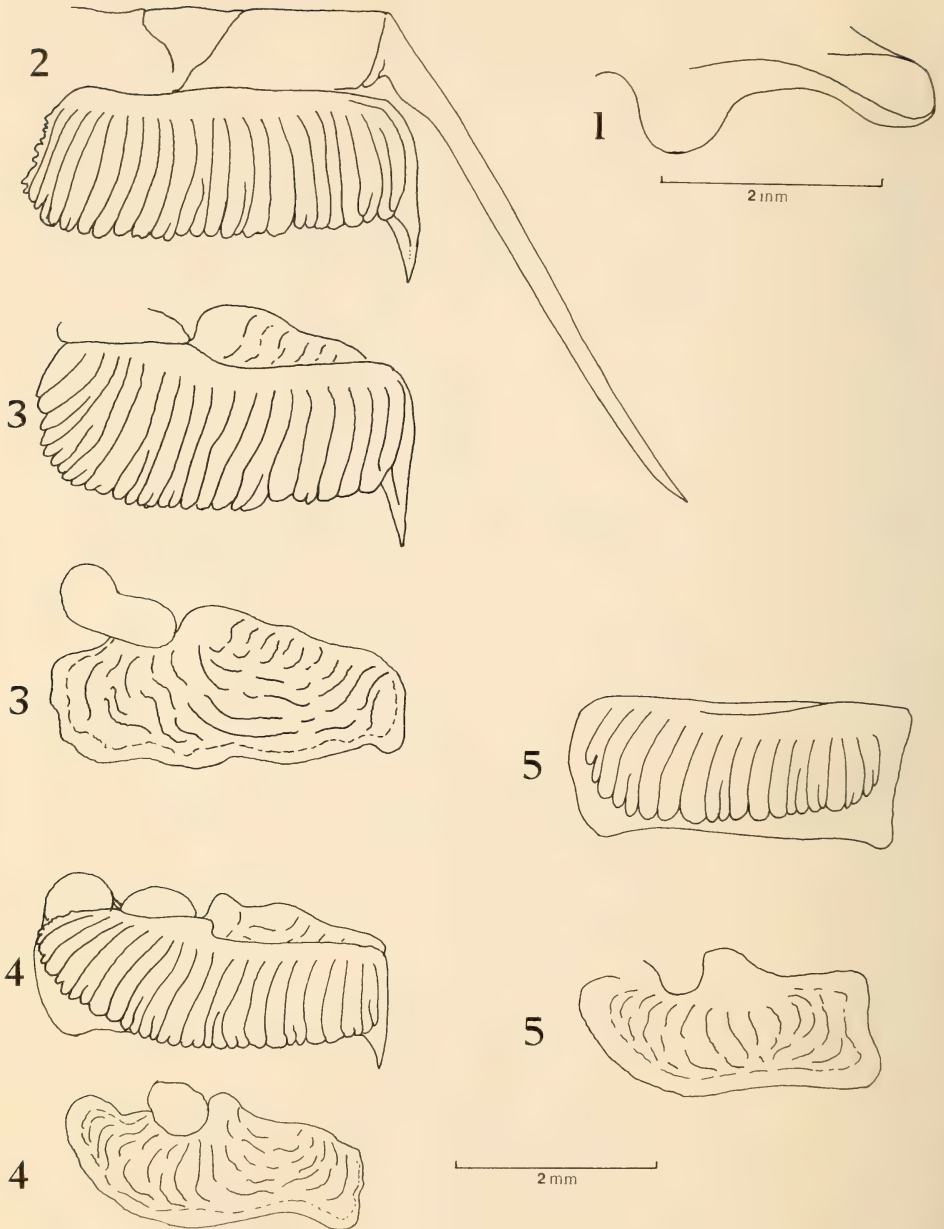


Fig. 6. *Tylos granulatus*. Pleopods one to five, male. (Two to five drawn to scale.)

modified to form long copulatory stylet medially, stretching posteriorly to level of fourth pleopods. Uropods valve-like, ventral, covering anal aperture, consisting of flattened basal portion with tiny setose endopod posteriorly. No sign of bilamellar uropod as mentioned by Stebbing (1910). Ventrally, segments three to five of pleon forming broad plates, those of segment five being antero-medially produced around the uropods, almost meeting in midline (Fig. 7a).

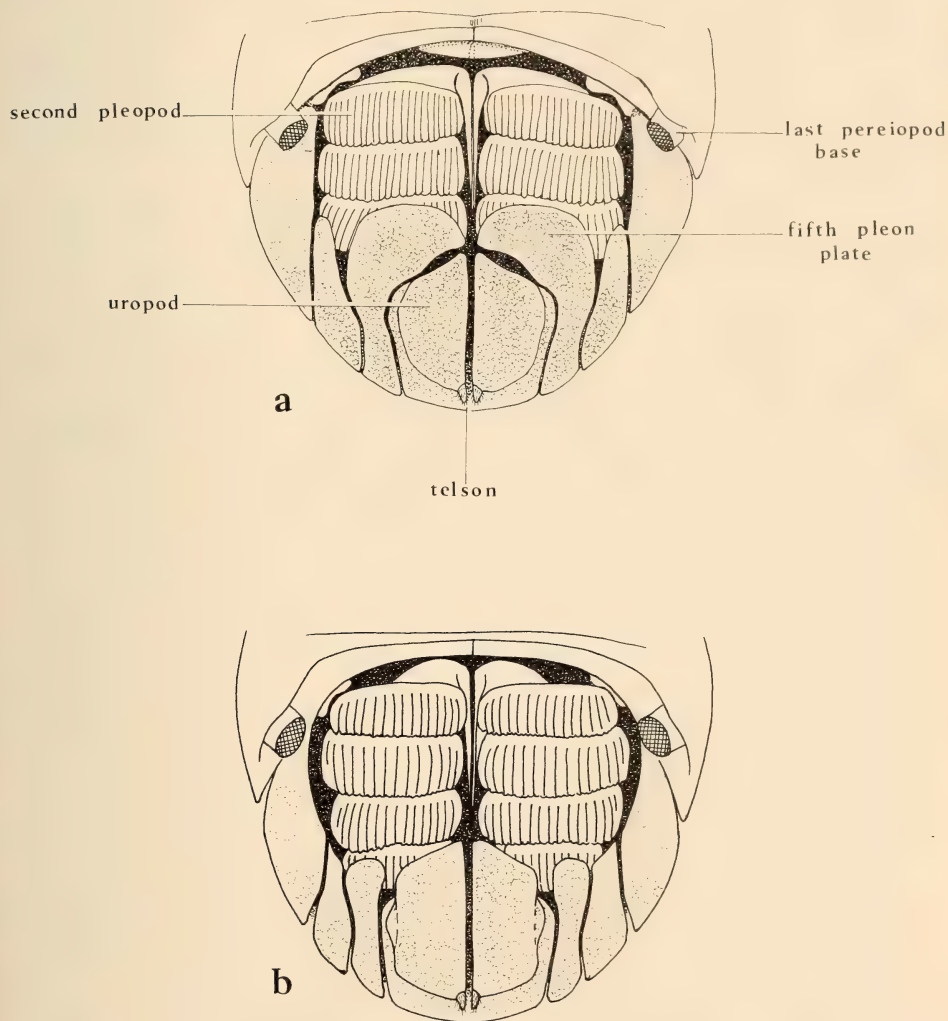


Fig. 7. Ventral view of pleon. a. *Tylos granulatus*. b. *Tylos capensis*.

Tylos capensis Krauss, 1843

Tylos capensis Krauss, 1843: 64, pl. 4, fig. 6. Budde-Lund, 1885: 276; 1906: 73. Dollfus, 1895: 352. Stebbing, 1910: 43. Barnard, 1932: 218, pl. 3, figs 14–18. Vandel, 1945: 227; 1952: 192.

Tylos granulatus (non Krauss), Collinge, 1945: 345.

Tylos incurvus Budde-Lund, 1906: 79, pl. 3, fig. 41.

Body oval-elongate, widest at fifth pereion segment. Integument chitinous, transparent, thick, minutely setulose, smooth. Membranous subintegumental layer bearing numerous branched chromatophores.

Head—evenly convex, bearing two compound eyes dorso-laterally, each composed of about 40 ommatidia. No distinct frontal line, but faint impressed line joining anterior margins of eyes, becoming obsolete medio-dorsally. Antero-ventrally the vertex narrowing between first antennae, giving way to broadly rounded frontal process, ventral to which, the broad clypeus, with labrum attached ventrally to it. Labrum not as asymmetrical as in *T. granulatus*. Narrow lateral genae embrace mandibular bases ventrally.

Head appendages—first antenna (Fig. 2d–e) consisting of single almost immobile segment, medio-dorsal to second antenna, dorsally flattened, roughly triangular, level with vertex surface, ventrally with broad articulating area, having socket-like depression near apex, containing numerous aesthetascs. Second antenna (Fig. 2f) stout, elongate, consisting of five basal segments plus flagellum of four smaller segments, terminal segment being proportionally larger than in *T. granulatus*. Second basal segment also differs from *T. granulatus*. Entire appendage setose. Mandibles powerful, heavily chitinized, left mandible (Fig. 8a) with incisor process consisting of three strong teeth, lacinia mobilis also of three powerful chitinous teeth, with setose lobe at base, followed by group of 10–12 penicillae, external to which, heavily setose molar process, terminated with rasp-like process. Right mandible (Fig. 8b) similar to left, differing only in lacinia mobilis, reduced, not heavily chitinized. Incisor process fits between lacinia mobilis and incisor process of left mandible. Labium bilobed and heavily setose, situated ventral to mandible, with median tongue-like setose lobe. First maxilla (Fig. 8c) bilobed, consisting of two endites. Outer lobe longer than inner, bearing setae on outer edge, with 10–12 curved terminal teeth of varying size, the larger teeth being heavily chitinized. Inner lobe terminated with three stout setose penicillae. Second maxilla (Fig. 8d) consisting of weakly chitinized broad plate, terminally heavily setose, with groove on inner face. Maxillipeds (Fig. 8e) meeting in mid-line, forming efficient lower lip, consisting of coxa and basopodite bearing broad palp and more slender endite. Palp with external surface scattered with blunt spines. Median edge divisible into three sections, reflecting fusion of three segments, each bearing numerous paddle-shaped modified spines. Endite smaller than palp, terminated with five setose penicillae.

Pereion—consisting of seven free segments, all except first bearing epi-merites (Fig. 4b), those of segments six and seven quadrate, those of other segments smaller, ventrally rounded. Seven pairs of pereopods present, first four

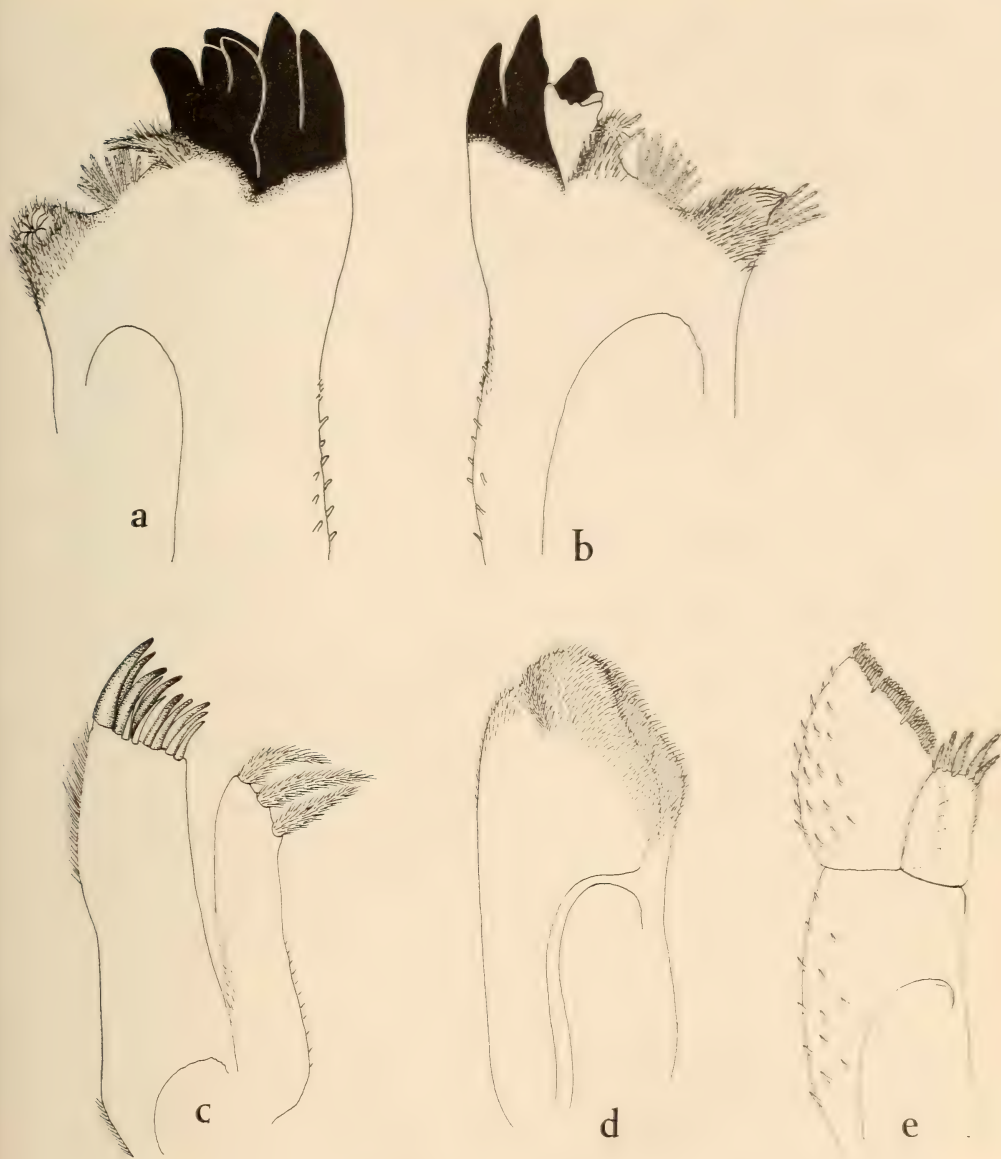


Fig. 8. *Tylos capensis*. a. Left mandible. b. Right mandible. c. First maxilla. d. Second maxilla. e. Maxilliped.

pairs forwardly directed, remaining three pairs posteriorly directed. Each pereiopod consisting of six segments, basopodite largest. Obvious angle between basis and rest of leg. Anterior four pairs with basis equal to merus + ischium + carpus in length. Merus with large dorsally rounded lobe. Carpus, propodus,

and dactyl together forming a claw. Numerous spines and setae on all segments, especially on more terminal ones. Posterior three pairs with basis equal to ischium + merus in length. Dactyl small; propodus, carpus, and merus stout, with strong spination.

Pleon—consisting of five free segments plus rectangular telson, latter broader than long. Five pairs of pleopods present, first reduced to slender lamella. Posterior four pairs consisting of basis, endo- and exopodite. Latter lamellar with numerous vertical slits, unlike *T. granulatus*, which has numerous folds. Endopods with irregular folds. Endopod of second pleopod of male modified to form median copulatory stylet, stretching posteriorly to level of fourth pleopod (Fig. 9). Uropods valve-like, ventral, covering anal aperture, consisting of single flattened lamina, with thickened ring-like inner portion, bearing tiny setose endopod posteriorly. Ventrally, fifth segment of pleon not produced antero-medially as in *T. granulatus* (Fig. 7b).

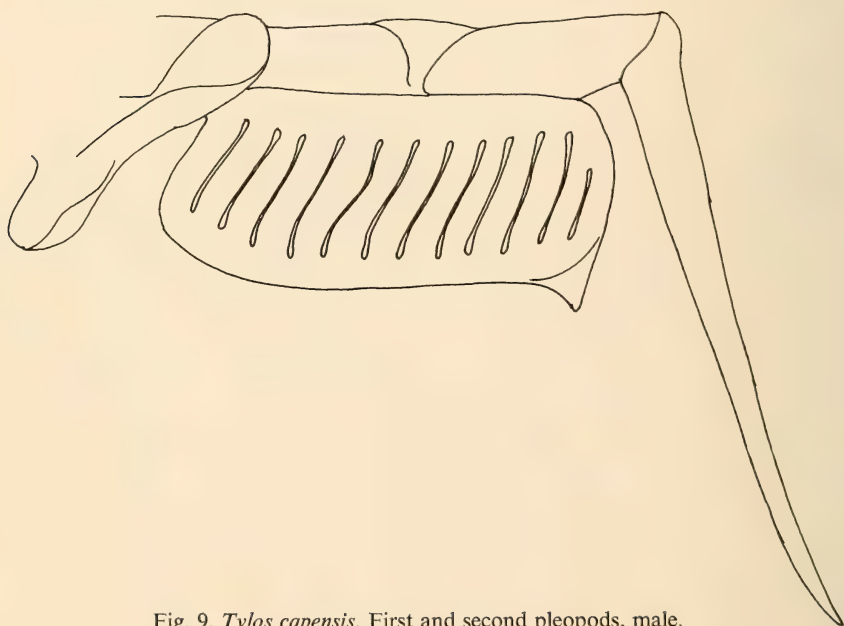


Fig. 9. *Tylos capensis*. First and second pleopods, male.

GEOGRAPHICAL DISTRIBUTION

Tylos granulatus

Krauss (1843) recorded his new species of *T. granulatus* from Table Bay. On the Cape Peninsula this species has been collected by the author at Hout Bay, Noordhoek, Olifantsbosch, Schuster's River mouth, and Witsandsbaai. Intensive collecting shows that the southern limit of the species is about 24 km from Cape

Point, and about 48–56 km from the first record of *T. capensis*, viz. Simon's Bay. Collecting along the coast of South West Africa has established the northern limit of the species to be in the region of the Ventura wreck site (19.10S., 12.37E.). This record extends the known range of the species by 480 km, the most northerly published record being Swakopmund (Panning 1924). Although the coast from this region north to the Kunene River was covered, as well as the southern coast of Angola, no further specimens were found. *T. granulatus* thus has a range of about 1 600 km. It was noted that towards the end of the northerly range the animals were not found on open beaches but were burrowing in the sand between rocks. A possible explanation for this was found in one of the limiting factors which prevent the northerly spread of the species. This is the ghost crab *Ocypode cursor* which inhabits sandy beaches and burrows into sand. This crab which occurs in large numbers, feeds voraciously on any organic material thrown ashore. Like the fiddler crabs of the same family, *O. cursor* seems to possess a tidal rhythm, and was observed to be active by day and at night. There can be little doubt that the presence of this crab presents a strong barrier to the isopods, feeding on the material which would normally form the food of *Tylos*. *O. cursor* occurs in the Mediterranean and along the entire west African coast. The southernmost record is 6.5 km north of Möwe Point, South West Africa. (19.23S., 12.42E.). The overlap of the two species is thus a matter of about 21 km, in which area neither is very abundant.

Haughton (1931), during a geological survey of the formations of the west coast, collected a fossil isopod from the oyster line of the diamondiferous deposit of Alexander Bay. The isopod was tentatively identified as *T. granulatus*. The hard matrix which concealed the ventral surface of the animal has now been drilled away. The granular surface together with the form of the ventral process of the fifth pereon segment establishes the first identification as being correct. The age of the oyster line is placed as mid Pleistocene. The species thus has a minimal age of 500 000 years. Taking rates of evolution into consideration it is probable that this species was already established at the start of the Pleistocene.

Tylos capensis

This species was first recorded by Krauss in 1843 from Table Bay, but this must have resulted from an error in labelling, as no record of *T. capensis* from the west coast has since been established. The species occurs eastward from False Bay. Budde-Lund (1906) records it from Simon's Bay, but this population has died out, perhaps due to naval and municipal development in the area. From Muizenberg eastward, the species occurs at most of the open beaches, including Strandfontein, Macassar Beach, Somerset Strand, Gordon's Bay, but is nowhere very plentiful. Along the south and east coasts the species occurs intermittently and is common in the Port Beaufort and Knysna areas. North of Port Elizabeth the occurrence could not be confirmed, but probably stops somewhere on the southern Natal coast. Barnard (1932: 219) makes the following statement: 'These animals form one of the most marked differences between

the faunas of the west and the east sides of the Cape Peninsula. If this separation of the two species, one from Table Bay northward and the other from False Bay eastward is proved to be a fact by further and more intensive collecting, it leads to the interesting though perhaps fruitless speculation as to why there was no transgression of the one species into the area of the other, when the sea was continuous across the present Cape Flats between Table Bay and False Bay.'

Method of dispersion

The actual method of dispersion of the species is still under dispute. Two main possibilities exist, viz. by sea or over land. Sea dispersion does not seem at all impossible. The survival of various sizes of *T. granulatus* in sea water was tested. The results are given in the following table.

(Temperature of water—17°C. Juveniles—under 20 mm length)

	No. Animals	Start	Comatose		Dead	
			No.	Time	No.	Time
Adults	15	0850	11	1600	15	1900
Juveniles	15	0850	13	1700		
			6	2000	5	2000
			10	0800 (next day)	14	0900 (next day)

Although by no means conclusive, it would appear that the juveniles have a greater survival time than the adults in sea water. The death of the adults is probably due to oxygen starvation, as the area of the pleopods is insufficient to take enough oxygen from the water by diffusion. The pleopod area in the juveniles is proportionally much greater than in the adults. From observations on beaches, it was seen that juveniles tend to feed lower on the beach than adults. The juveniles are usually found on the debris lines, the adults only occasionally. On the debris lines there is the danger of powerful waves swamping the feeders. This was often seen at Blouberg (an area where intensive observations were carried out). The juveniles roll up into a ball when exposed to an incoming surf. This rolling encloses a bubble of air between the setose pereopods, making them buoyant. The result of being caught in the surf is that they are deposited on the beach at the new debris line, along with pieces of food. This would seem to be a useful adaptation for food-finding. It is possible that with a very powerful wave, instead of being left behind on the sand, the juveniles are swept to sea. A survival of 12 hours at sea would give them a good chance of being thrown up on an adjacent beach. This would explain the distribution of the species in such places as Lüderitzbucht, where small sandy bays alternate with steep rocky outcrops, over which it would be impossible for the animals to climb. It is interesting to note that Menzies (1952) records having taken two almost adult specimens of *Tylos punctatus* in a surface plankton haul in Newport Harbour, California.

Menzies notes that *T. punctatus* has a very discontinuous distribution along the coast, being found around bays and estuaries, and never on open coasts. He concludes that this record may strengthen the hypothesis that such discontinuous distribution can be accounted for by the animals being carried by ocean currents.

The behaviour of adults caught in the surf is interesting. As the incoming surf sweeps over them, they 'flatten out', allowing the water to wash over them and then back. As soon as the water has receded, they can be seen to move rapidly up the beach, out of the reach of the waves.

Land dispersion is almost certainly used under certain conditions. The most obvious example is that of the Orange River mouth. Brown (1959) noted that when the river mouth was open to the sea *T. granulatus* was to be found in the sand on the southern bank. In March 1968 the mouth was completely blocked by an extensive sand bar, along the entire length of which the isopods were to be found. This sand bar had been in existence for two years since the last flooding of the river. This latter event occurs spasmodically, sometimes consecutively for several years, or more usually once every two or three years. Between floodings the sand bar is built up. Within two years, *Tylos* had thus colonized a sand bar about 3 km long. The most obvious method of colonization would be by moving in from the undisturbed banks of the mouth. Since the Orange River population is to be found on the landward side of a crest on the beach, it is unlikely that the alternate method of colonization occurs here.

HABITAT

Both *Tylos granulatus* and *T. capensis* inhabit sandy beaches of the coasts of southern Africa. On these beaches the animals are exposed to numerous environmental factors, the influence of each varying in importance to the animals. These factors include the sand itself, the sea and its tides, the water table in the sand, temperature fluctuations, humidity, light, precipitation, in addition to several extraneous factors. Although some of these factors are discussed separately below, it must be borne in mind that they all interact to produce the overall habitat.

TYPE OF BEACH

Tylos granulatus

After numerous observations, it can be said that this species frequents beaches which almost invariably are exposed to strong wave action, uninterrupted by rocks. This type of beach is common along the west coast, all the localities listed in the section on distribution being of this type. The preference for the exposed beach could clearly be seen in several places, particularly in Griffith's Bay, Lüderitzbucht, where there is a small exposed beach, as well as a long stretch of low rocks. Behind the latter in the HWS to HWN region, is a band of sand similar to that of the exposed portion. *Tylos* was found on the exposed part, up to the edge of the rocks but not in the sand behind the rocks.

The slope of the beach would also appear to be of some importance. The populations are spread out on flat beaches, where the high tide floods a large area. This was clearly seen at Groenriviermond and Stormvogelbucht. On beaches with a moderate gradient such as Blouberg (slope of $1/8$) the population is still fairly outspread. At the mouth of the Orange River, where the population inhabits the sand bar at the actual mouth of the river, the beach has a slope of $1/4$, and the animals are found on the landward side of the crest. The latter is at the HWN mark. Presumably to live on the seaward side of the crest would expose the animals to too much wave action.

Tylos capensis

Unlike *T. granulatus*, this species does not seem to be as selective in its choice of beach, being found on exposed as well as on sheltered beaches. At Strandfontein, an exposed beach with a very gentle slope (about $1/20$), the population is spread out along the HWS region. At the mouth of the Breë River the population is found on a short steep beach ($1/6$) within the actual mouth of the river. Although quite sheltered, there is still some wave action, mostly due to wind on the open expanse of water. At Knysna the population is found at the lower reaches of the lagoon estuary, again on a short steep beach, but where the wave action was very slight.

SAND

Tylos granulatus

The actual type of sand in which *Tylos* burrows is very variable, and it would seem that the animal has a wide tolerance of sand grain size. At Griffith's Bay and Groenriviermond the sand is very fine, forming a soft mud when saturated with water. The Blouberg sand varies from fairly fine white quartz grains to layers of coarser mixed grains and shell fragments, very compacted. The sand at the mouth of the Orange River is dark brown, consisting of grains of garnet, amethyst, granite, fairly coarse and very friable. At Blouberg the area inhabited by *Tylos* ends with the start of a large reef of rock. In this area the beach consists of fine pebbles all about 2–3 mm in diameter. No animals are to be found here, but 20 animals transferred to this area all burrowed to a depth of about 120 mm. The most unusual substrate in which this species was found was observed at Griffith's Bay, where the upper 127 mm consisted of fine white sand. This gradually gave way to a 76 mm layer of grit and small pebbles. Below this was a 152 mm layer of limpet and mytilid shells, followed by large rocks and shells to a depth of 610 mm. Animals are found in this very coarse substrate to a depth of about 305 mm.

Tylos capensis

As in *T. granulatus* this species has been found in a variety of sand types, viz. very fine quartz sand with shell fragments at Strandfontein, friable fairly

fine sand at the mouth of the Breë River, and uniformly fine sand at Knysna.

T. latreillei from the Mediterranean and North American coasts appears to be very different from both South African species in its choice of habitat. Arcangeli (1953) remarked that *T. latreillei* avoided beaches of fine sand, nor was it found at river mouths where the sand tended to mud, as its pereopods impaired its progress. Instead, it inhabited crevices of rocks, or lived amongst stones and pebbles, or sometimes in coarse sand. *T. punctatus* of the North American west coast also differs from the southern African species in choice of habitat. Menzies (1952) notes that *T. punctatus* inhabits sandy beaches, but is found under logs and debris where the sand is usually dry and seldom inundated by the high tides.

TIDES AND THE WATER TABLE

Tylos capensis and *T. granulatus*

The importance of the tides is more fully discussed in the section dealing with rhythmicity. Arcangeli (1953) in his discussion of the ecology of *T. latreillei* remarks that this species is 'indifferent' to the tides—quite the opposite to the present species. The water table varies with the tides but is unlikely to have any direct effect on the animals. From Figure 17 of the transect of the Blouberg area studied, it can be seen that the water table is too far below the level to which the animals burrow to influence them.

WIND AND PRECIPITATION

Tylos capensis and *T. granulatus*

Light rain and mist have no apparent effect on the animals, while gale force winds do not seem to interfere with their feeding activities.

TEMPERATURE

Tylos capensis and *T. granulatus*

As can be seen from Figure 10, the temperature within the sand at the level of the high tide mark is subject to less fluctuation than the surface sand. As under normal conditions no extremes of temperature are experienced, it seems unlikely that the daily temperature changes have any influence on the animals. Seasonal temperature changes are of greater importance and are probably involved in the timing of the reproductive cycle.

HUMIDITY

Tylos capensis and *T. granulatus*

As *Tylos* breathes by diffusion of gases through modified pleopods which are exposed on the ventral portion of the pleon, humidity is of great importance. The habits of the animal thus preclude any serious exposure to desiccating conditions. The sand, even a few metres above the HWS mark, has a relative

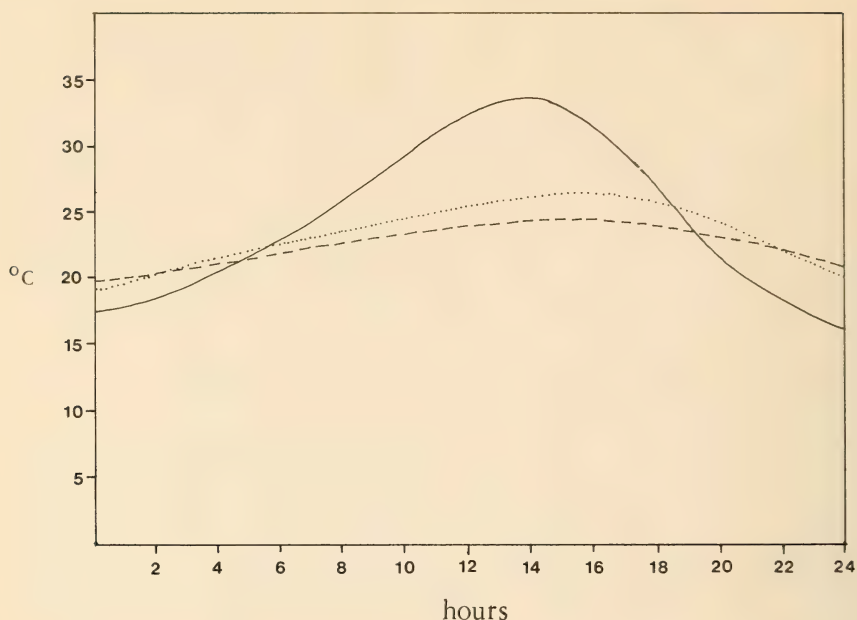


Fig. 10. Temperature changes over 24 hours in midsummer at Blouberg. — surface temperature. temperature at 300 mm. — — — temperature at 450 mm.

humidity of more than 90% at 75 mm below the surface. The upper 75 mm of sand is frequently dried out during the day by sun and wind, but as no animals are in this layer during the daylight hours, this presents no danger. At night with the drop in temperature, spray from the sea together with any dew deposition keeps the air close to the sand almost saturated with water vapour, thereby preventing desiccation.

LIGHT

Tylos capensis and *T. granulatus*

It is not possible for sunlight to penetrate more than 25 mm below the surface of the sand; sunlight would thus have very little direct influence on the animals. When exposed to sunlight, the animals rapidly burrow into the sand, and can be said to be strongly negatively photosensitive. When not feeding, both species react to both white and coloured light by becoming immobile, but bright white light has little immediate effect on feeding animals.

EXTRANEOUS FACTORS

During week-ends, both areas studied form part of a popular beach, and are often continuously trampled. This does not seem to have any effect on the nightly emergence of the animals.

Oil pollution

This was noted at the Blouberg population studied, when several observations were made. Crude oil from the ballast tanks of a tanker washed ashore on 7 February 1970. The following day was a spring tide, the result being that the beach was covered with oil from the water line to the HWS mark (Fig. 11a). At



Fig. 11. a. Oil pollution at Blouberg. b. Exit holes through thick oil.

the lower levels wave action tended to froth the oil, which was therefore not very thick. Higher up the beach the oil formed a thick solid deposit. Low tide on the night of the 7th was at 2225 hours, when not many animals emerged. Almost all the animals which did emerge were killed, death probably being caused by clogging of the pleopods and a consequent arrest of respiration. About

30 dead animals and about the same number of exit holes were found. On the night of the 8th, low tide was at 2303 hours, when numerous animals emerged (Fig. 11b). Where the oil was not very thick, the animals returned at the high water mark (Fig. 12a). Where the oil formed a thick layer at the high water



Fig 12. a. Return mounds on thin oil layer. b. Return mounds amongst vegetation in low sand dunes, well above HWS.

mark, a few animals returned at a lower level. Many moved above the high water mark, into the low sand dunes, and burrowed amongst the vegetation (Fig. 12b), something not seen before. Of the animals which entered the sand through a thin layer of oil, several were dug up. No trace of oil on the bodies other than at the tips of the pereopods between the bristles could be seen.

Presumably the corkscrew action used in burrowing rubbed off any adhering oil. A food problem was posed as almost all the seaweed was oil-covered. Above the high water mark, very little vegetable matter was present other than the actual dune plants, some of which were eaten. Humidity did not pose any problems, in spite of the fact that the dry surface layer of sand was deeper than at the high water mark. After about three weeks the animals returned to their usual level on the beach, as some of the oil had been removed, while the thinner layers had been covered by wind-blown sand.

LOCAL DISTRIBUTION AND BURROWING

The local distribution of *Tylos* may be discussed under three headings, viz. distribution along the beach, i.e. parallel with the sea; distribution on the beach at right angles to the sea; vertical distribution in the sand. The actual distribution of *Tylos* on any section of beach can be judged by the spread of either the exit holes or the return mounds. This judging of the population spread is easy at the time of spring tides, when the animals emerge and return on clean-swept sand. At the time of neap tides, however, the sea does not remove each day's mounds and holes. An overlapping then occurs, obscuring the distribution. Strong winds also flatten mounds and fill holes, obscuring the spread. A more definite check can be made by digging a trench up the beach, or by actually observing the animals emerging at night.

DISTRIBUTION ALONG THE BEACH

Tylos granulatus

The most important fact to emerge from prolonged observation of a population, is that it is, as a whole, clustered mainly around the high water mark. An explanation for this is that food is deposited at the high tide mark. During spring tides, algae which have been torn loose are left far up the beach. The *Tylos* population at high water of springs is thus far up the beach. At the same time, if a long stretch of beach is observed (about 500 metres) it can be seen that the population is split up into separate clusters along the HWS mark (Fig. 13a). As the height of each tide decreases after the spring tide, the population spreads out, some individuals following the high tide mark as it progresses down the beach, others remaining higher up. The result is that whereas at spring tide the population is split into clusters, at neaps it is outspread and forms a continuous band along the beach (Fig. 13b).

Tylos capensis

Although never as abundant as *T. granulatus*, this species shows a similar distribution along the beach, being clustered high up the beach at springs, and very spread out at neaps.



Fig. 13. a. A cluster of return mounds of *T. granulatus* at HWS, Blouberg. b. Blouberg at neaps. Exit holes at left. High tide line at centre marked by blocks of wood, etc. Return mounds at right.

DISTRIBUTION ON THE BEACH AT RIGHT ANGLES TO THE SEA

Tylos granulatus

The term 'at right angles to the sea' is used in preference to 'vertical zonation' as in this case the situation is complicated by the additional distribution vertically in the sand, and by the change in spread with the change in the height of the high water mark. The spread of the population up the beach appears to be related to the range of the high tide. On a beach which has a very flat high water area, such as Groenriviermond or Stormvogelbucht, the population is spread over an area about 100 metres in width. At Blouberg where the beach has a slope of about 1/8, the population inhabits an area about 20 metres in width. Figure 14 indicates the concentration of animals in two half square metres. Set (a), 10 metres above HWN, contained five animals; set (b) at HWN, contained 60 animals. Ten metres below HWN no animals were present.

The Orange River population is unusual in that it is situated on the landward side of a sand ridge which slopes towards the river pools. Here the area occupied is about 30 metres in extent.

Tylos capensis

A similar situation prevails with this species. At Strandfontein, with a slope of about 1/20, the population is spread over about 40 metres. The Breë River population on a much steeper slope occupies an area with a width of about 10 metres.

VERTICAL DISTRIBUTION IN THE SAND

This was obtained by excavating random half square metres. (This area was preferred to that of a full square metre, due to the time needed to complete an excavation.) The volume of sand under this half square metre was divided into layers each 80 mm deep. The distribution of animals in each 80 mm layer was then plotted on rectangles. This excavation was done in each case until no further animals were encountered. The time of day at which the excavation was done was recorded. These results may be seen in Figures 14 to 16.

Tylos granulatus

In Figure 14a-c it can be seen that in the late afternoon the majority of animals are between 80 and 240 mm below the surface. At sunset, the majority are distributed from just below the surface to about 160 mm down. At Ysterfontein (Fig. 14), a beach similar to Blouberg, at about midday the majority are from 240 to 320 mm below the surface. Figure 15a-c of the Orange River mouth shows the distribution of the animals over a length of about 30 metres of beach. The positions of the half square metres may be seen on Figure 17a. The juveniles appear to be concentrated in the upper layers of the sand. As at Ysterfontein and Blouberg at midday, the adults are concentrated at a depth of 160 to 320 mm below the surface. This is again seen in Figure 16d of Agate

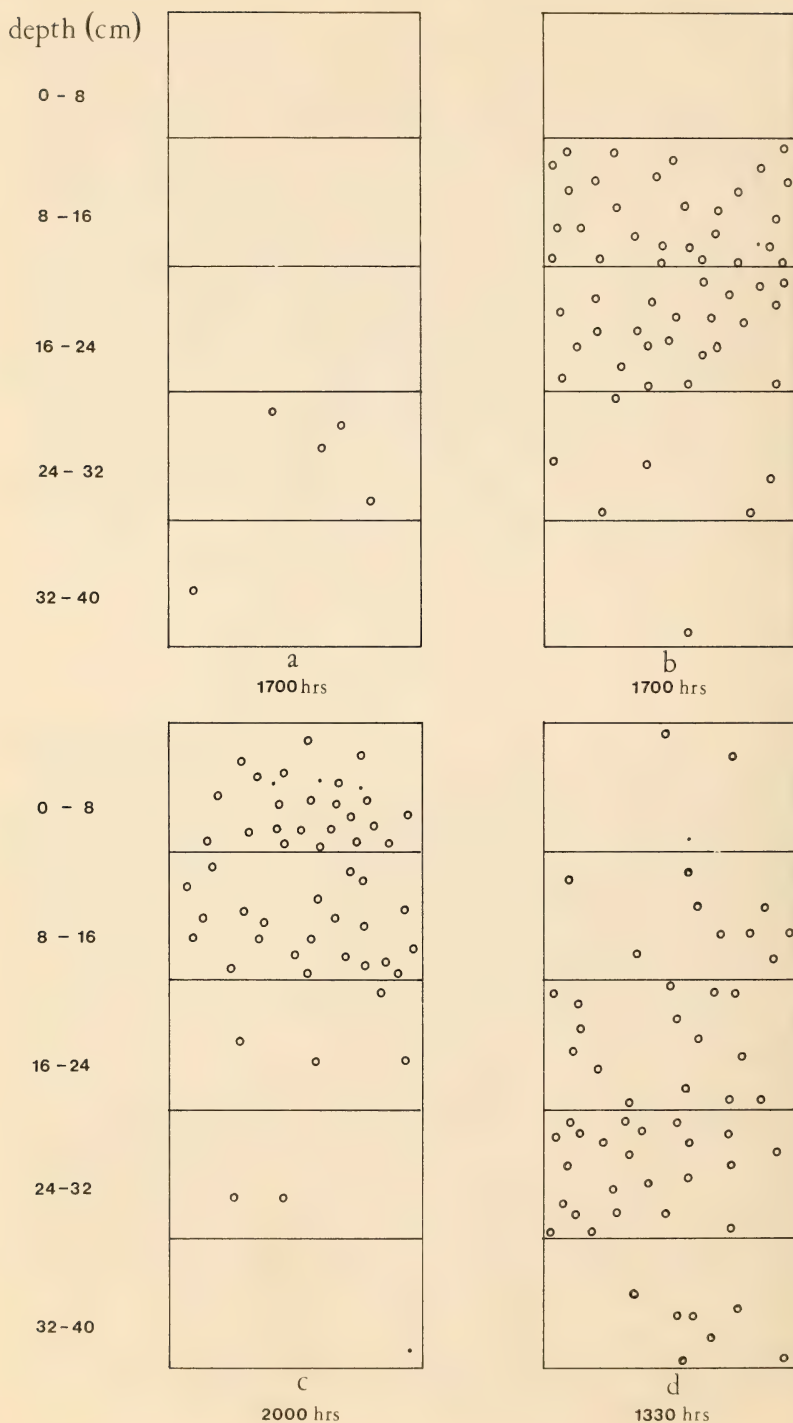


Fig. 14. Vertical distributoin of *Tylos granulatus*. a-c. Blouberg. d. Ysterfontein.

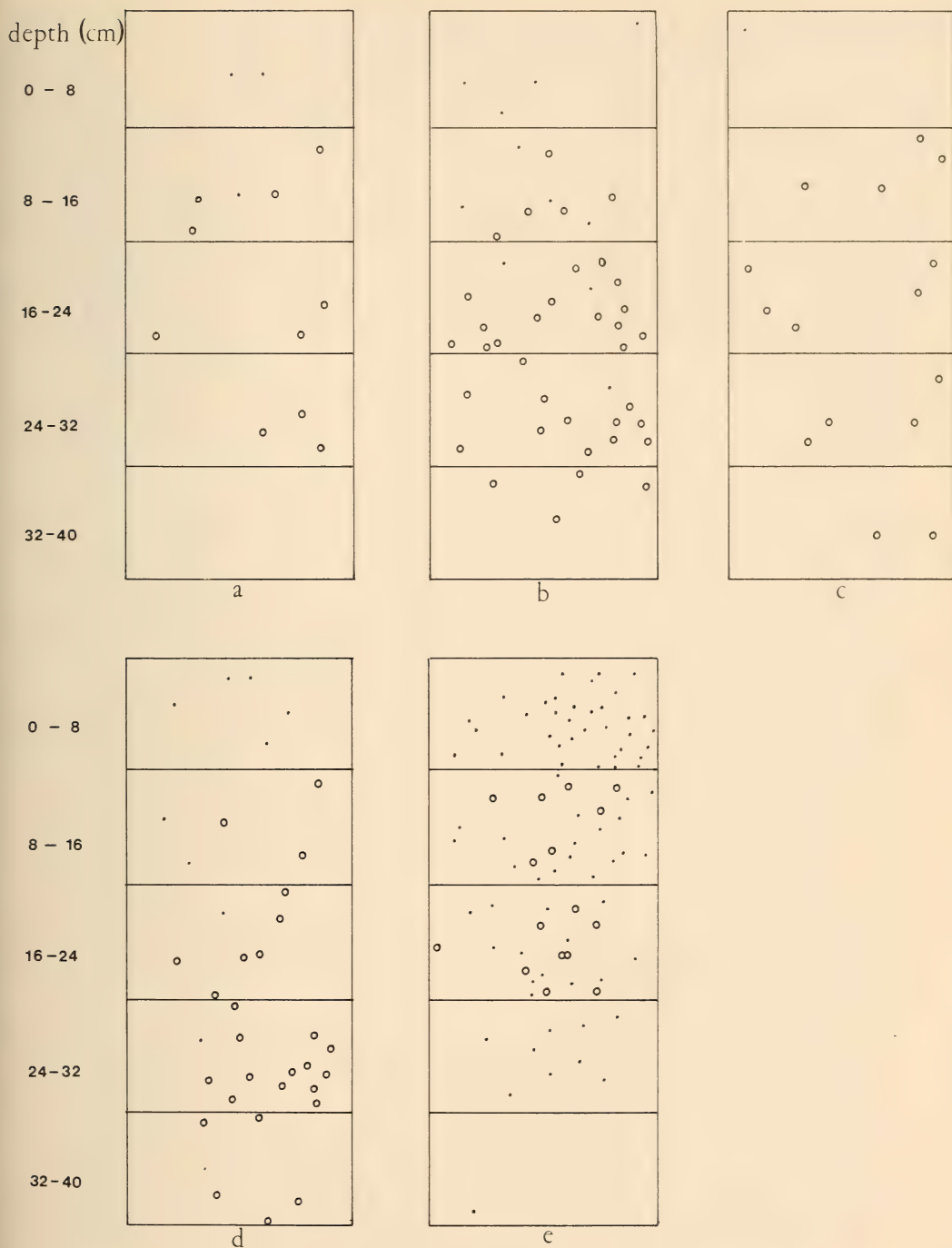


Fig. 15. Vertical distribution of *Tylos granulatus*. a-c. Orange River mouth sand bar. d. Agate Beach, Lüderitzbucht. e. Griffith's Bay, Lüderitzbucht.

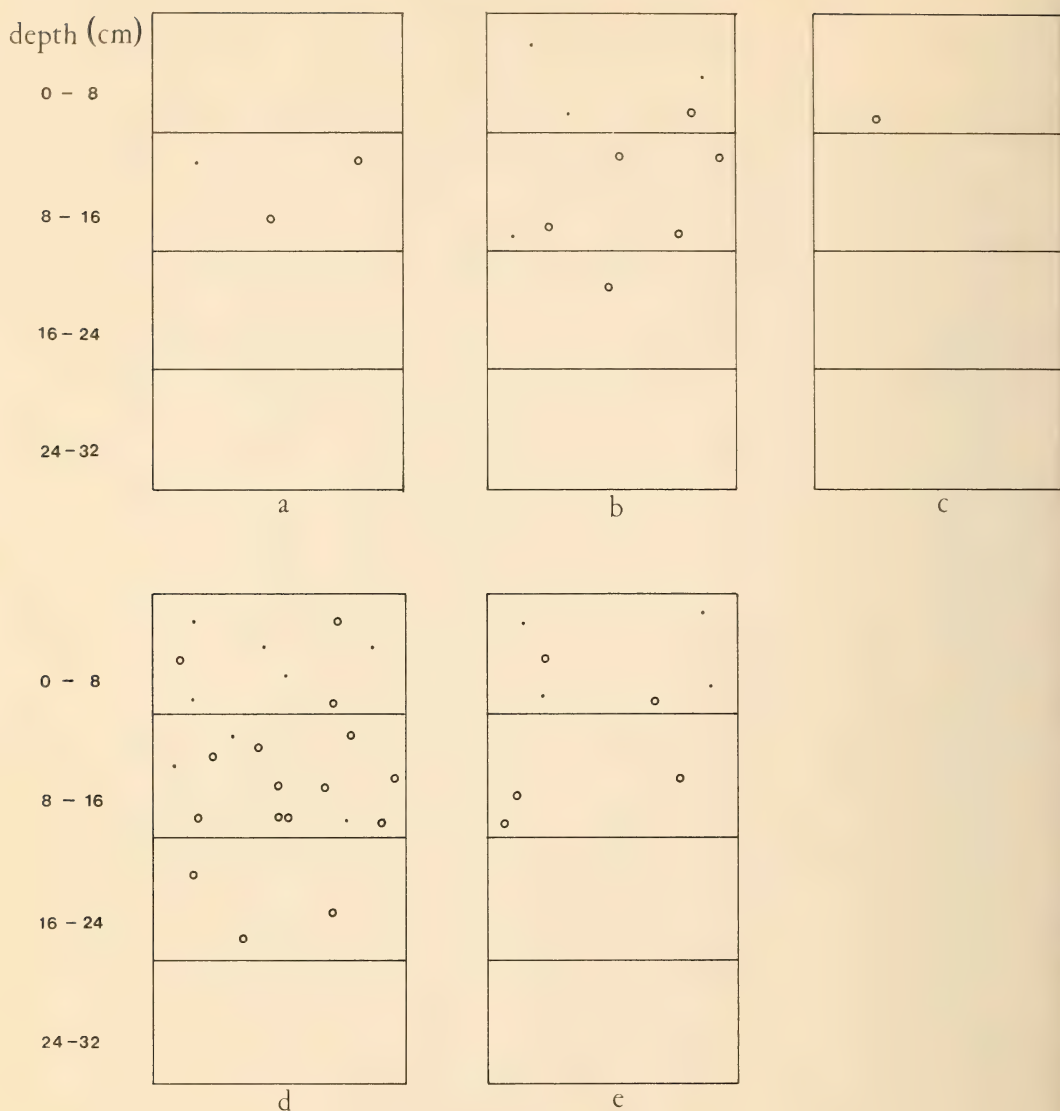


Fig. 16. Vertical distribution of *Tylos capensis*. a-c. Strandfontein. d-e. Breë River.

Beach, Lüderitzbucht, where the juveniles are found in the upper layers. Figure 15e of Griffith's Bay, Lüderitzbucht, represents an unusual vertical distribution which can only be satisfactorily explained by reference to the substrate in which the isopods were found. From the figure it can be seen that whereas the adults are limited to the depths of 80 to 240 mm, the juveniles, although concentrated in the upper 80 mm, are spread throughout the sand to a depth of 320 mm.

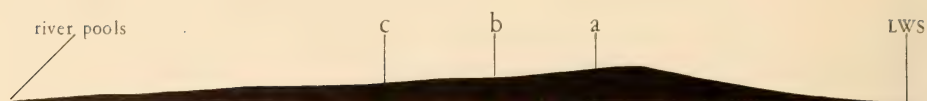
For midday the adults are unusually close to the surface, but they could not have burrowed deeper. The fine sand penetrated to a depth of 120 mm but gradually gave way to grit and small pebbles to about 200 mm. This layer was replaced by a deeper layer of large stones and shells. The juveniles could move between these large objects, but not the adults.

Tylos capensis

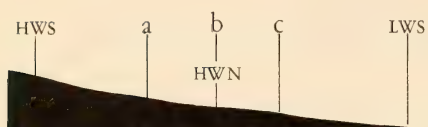
The vertical distribution of this species was also investigated by means of half square metre excavations, at both Strandfontein and the Breë River (Fig. 16a-e). Beach profiles may be seen in Figure 17c-d, on which the positions of half square metres are indicated by the letters 'a, b, c.' While at no time abundant, it would seem that this species seldom burrows to a depth of more than about 200 mm.

METHOD OF BURROWING

Burrowing was observed on the beach as well as in the laboratory. Captive animals were observed in large perspex/glassfibre containers, as well as in limoria. These latter being 30 mm wide, just allow an adult *Tylos* space to turn a complete circle when digging almost vertically downwards. This meant that the animals were always visible from either of the glass sides at any one point. All observations were done in the dark, using a torch at brief intervals, so as to disturb the animals as little as possible. The sequence of actions used in burrowing is as follows: the animal scoops out a hollow in the sand, using the anterior three pairs of pereopods. These pass the sand on to the posterior four pairs of pereopods, which push the sand backwards, to form a little heap behind the animal. The animal then moves sideways, through an angle of about 45°, digs out more sand with the first three pairs of pereopods, pushes it back with the posterior legs, and forms another heap of sand next to the previous one. This sequence continues, usually five to seven pushes of sand, followed by a pause of about a minute. Each short burst of digging takes the animal a little deeper into the sand, as it moves laterally (usually anti-clockwise) after each push. The overall movement is a helix-shaped path passing vertically through the sand. One complete turn of the helix represents eight or nine backward pushes of sand, and takes the animal about 30 mm into the sand. On the surface this complete turn can be seen as an irregular cone of sand, having eight or nine small peaks if the sand is moist and the grains clinging. When the animal starts digging, the antero-posterior plane is horizontal, but as it progresses, this plane tilts upwards, so that once the animal is in the sand, this plane is vertical. Once below the surface, the backward pushing of the posterior pereopods closes the hole. As the sand is usually moist below the surface the backward pushing tamps the sand, preventing it from falling back and hindering progress. The actual speed of digging varies, depending on the number of rests. Timing of six animals shows that the usual speed is about 200 mm/12-15 minutes. Once the animal has reached the 'desired' level, it moves around, flexing the pereopods. This



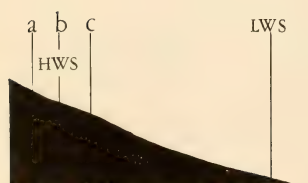
a. sand bar at Orange River mouth



b. Blouberg



c. Strandfontein



d. Breërivier

scale: 1 div = 10m

Fig. 17. Beach profiles. LWS—Low water of springs. HWN—High water of neaps. HWS—High water of springs. a. Orange River mouth sand bar. b. Blouberg. c. Strandfontein. d. Breë River.

causes its rounded dorsal surface to press against the sand, thus forming a chamber only slightly larger than itself. Once this is done, the animal curls up and remains in this position. Usually with the eyes ventral, until the time of emerging approaches.

It was sometimes seen that an animal will start digging on a mound, i.e. where another animal has gone down. The surface counts of mounds thus need not give an accurate indication of the number of animals below the surface. For example, at Lambert's Bay the surface count for a random half square metre was 55 mounds, but excavation yielded about 120 adults. Although several animals may enter the sand at the same point, once in the sand they separate and emerge from separate holes.

The actual time taken to emerge, once the animal becomes active, is not known, but is probably much longer than the return digging. This is inferred from observations made at different times of the day. For example, at 1700 hours most of the adults are 80 to 240 mm below the surface. At 2000 hours at the same locality, most of the adults are from just below the surface to 160 mm below. The animals may dig upward either following the path made by their entry or may follow a fresh path. Once the animal reaches the surface and the eyes are exposed, it pauses (Fig. 18a). This pause was observed in all emerging animals, varied in duration, but was usually between 2–15 minutes. Once the animal has left the burrow, its point of exit is marked by a circular hole up to 30 mm deep (Fig. 18b). The animal then immediately starts a rapid apparently random perambulation, stopping only when food is encountered.

From this study of the local distribution and burrowing of both species of *Tylos* the following facts emerge:

1. *Tylos* usually burrows close to the high water mark.
2. At HWS the population is high on the beach and clustered.
3. At HWN the population is lower on the beach and outspread.
4. The animals are distributed in the sand up to a depth of 500 mm in the case of *T. granulatus*, 200 mm in *T. capensis*.
5. The animals burrow with a spiral movement.
6. Re-entry into the sand leaves a cone-shaped mound on the surface.
7. The speed of return to the surface is slower than the speed of re-entry into the sand.
8. Exit points are marked by a shallow circular hole.
9. The animals sometimes return via a path made by another animal.
10. All digging is approximately vertical.

FOOD AND FEEDING

The section dealing with feeding and related topics in *Tylos* has been divided into several sections, viz. actual feeding, i.e. the obtaining of the food, the food preferences, the structure of the alimentary canal, and the actual process of digestion.

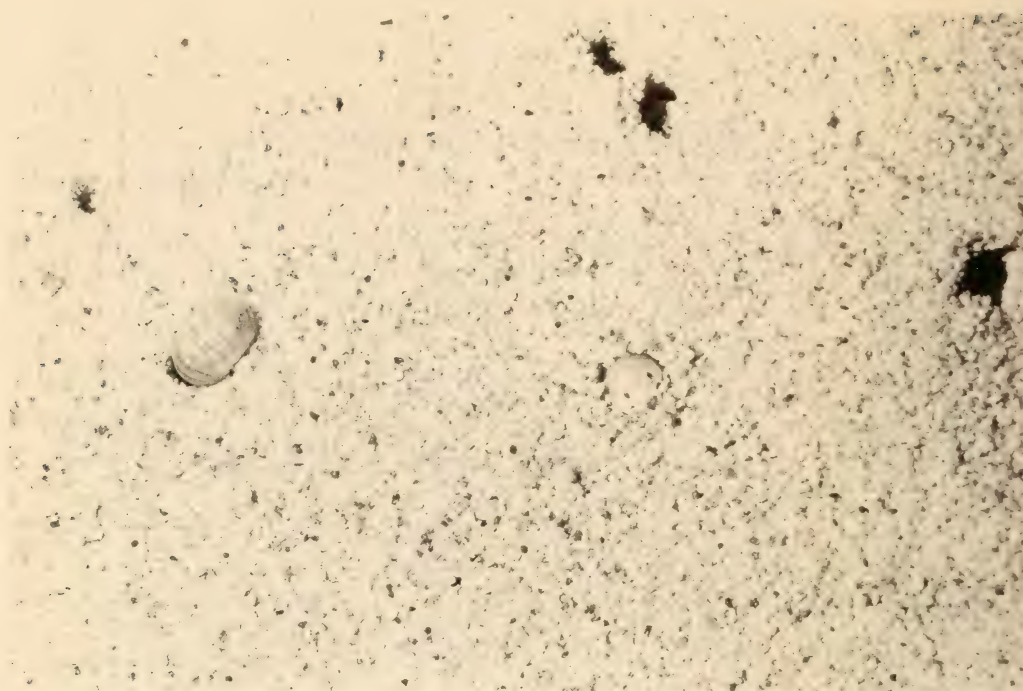


Fig. 18. a. *T. granulatus*. Animal at left starting to burrow, animal at right just emerging. Exit holes at upper right. b. Numerous exit holes of *T. granulatus*.

ACTUAL FEEDING

The feeding of both *T. capensis* and *T. granulatus* is confined to the brief period (two to three hours) that the animals are emerged. It was found that *Tylos* tends to burrow around the high tide mark, moving down the beach as the height of successive tides drops, or up the beach as the level approaches that of spring tide. This is a behavioural adaptation connected with food supply, as any floating debris including sea weeds and dead animals will be left on or near the high tide mark. The mouthparts are adapted for rapidly cutting pieces of food. The gut, particularly the midgut portion, is very capacious. Both these factors allow the animal to eat a maximum amount in the time available. A very rough measure of the amount eaten in the period emerged may be obtained from the following data (see Table 3). Ten specimens of *T. granulatus* were captured as they emerged to feed, weighed, marked, and allowed to feed. These animals were again captured at the end of the feeding period, reweighed and their length measured. They were then killed and the volume of the food in the gut measured by displacement. From this it was found that the animals ate up to 25% of their body weight in the two-hour period involved. A similar situation was found to apply in *T. capensis*.

From observations of animals feeding, a list of foodstuffs was compiled, which is summarized in Table 4. From a survey of the food consumed by the isopods it can be seen that both species are omnivorous, but with a bias towards an herbivorous diet. In this, *T. granulatus* and *T. capensis* resemble the European *T. latreillei* which Arcangeli (1953) describes as feeding on 'decomposed matter'.

From observation it was seen that the majority of adults feed almost exclusively on algae, while the juveniles (less than 15 mm in length) feed mainly on animal matter. The adults which are found around the high water mark feed mainly on the larger brown algae thrown ashore, along with the epiphytes on these algae. It would seem from the table of food matter, that the red algae form the major portion of the food, but relative sizes must be borne in mind. Whereas most of the red algae are small flattened plants, seldom more than 100 mm in length, the brown algae are often several metres in length, with massive stipes. All three brown algae recorded are large plants.

When feeding on *Macrocystis* it was noted that the animals eat only the flattened strap-like portions of the thallus. This results in large piles of stipe being left on the beach, along with the inflated basal portions of the fronds (Fig. 19a). When feeding on *Laminaria* or *Ecklonia* it was noted that the animals congregate on the flattened blades which are eaten from the edges (Figs 19, 20). This preference for the flattened portions results in a typical grazing pattern, i.e. many stipes denuded of fronds (Fig. 20a). Should food be scarce, however, the animals can be seen feeding on the stipes of these two algae. An examination of the mouthparts makes it obvious that feeding on a broad solid surface with no edge on which to start is more difficult than feeding on flattened straps. Animals feed apparently indiscriminately on both moist and dry algae. Feeding



Fig. 19. a. *T. granulatus* feeding on blades of *Macrocystis*. b. *T. granulatus* concentrated around the blades of *Ecklonia*.



Fig. 20 a. Grazing pattern of *T. granulatus*. Denuded stipes in foreground, ungrazed stipes in background. b. *T. granulatus* feeding on the edges of *Laminaria* blades.

on dry algae, although seemingly difficult, can be explained. During the day the kelp is tough and leathery, but at night with no heat for evaporation and with moisture being deposited by dew and sea mists, the fronds soften slightly.

Although the juveniles are occasionally found feeding with the adults on the larger brown algae, the majority are found on the debris lines. Their presence here is to some extent due to a behavioural trait. The juveniles are usually found lower down on the beach than the adults, and often are caught in the waves. Unlike the adults which flatten out to let the water flow over them, the juveniles roll up into a ball, thereby capturing a bubble of air between the pereopods, making them buoyant. They are carried up the beach by the wave and are left behind on the debris line along with their food. This latter in the juveniles seems to consist mainly of animal matter. If on any one night the number of juveniles feeding on different material is observed, the following sort of numbers may be obtained: jellyfish fragments 17, *Ulva* 5, other substances 5. Should any fish or *Physalia* be washed ashore, larger numbers of juveniles are found feeding on them.

FOOD PREFERENCES

To indicate very approximately the food preferences of *T. granulatus* (presumed to be similar to *T. capensis*) the following procedure was followed: Six containers measuring 400×200 mm and 100 mm deep were filled with damp beach sand to a depth of 80 mm. Ten adult *Tylos* were placed in each container. Shallow containers were used to allow for a minimum of time to be spent by the animals in burrowing, and for their easy removal. The containers were kept under normal external light and temperature conditions, sheltered from rain. The containers were left undisturbed for three days, during which time no food was provided. Thereafter food of various types, having been weighed, was placed randomly on the sand in the containers at 1730 hours. A container without animals was used as a control. At 0800 hours the following morning, those pieces of food which had been eaten on were reweighed, the percentage water loss also calculated. The percentage water lost from the remaining piece of food was added to the weight of the remaining piece of food. This total was then subtracted from the original weight of the food. In the first set of tests, the animals were taken from a beach almost devoid of food. The animals were then starved for a further three days. When food was then provided on two consecutive days, those animals which emerged ate large amounts. After this, less food was eaten at any one 'sitting'; the food was then provided at intervals of two to three days.

First choice

Roughly equal amounts (between 0,8 and 2,5 g) of the following six substances were provided: two brown algae—*Macrocystis* and *Laminaria*, one green alga—*Ulva*, one red alga—*Gigartina* sp., cabbage, and fresh fish. All these substances have been observed to have been eaten by *Tylos* at the Blouberg

population studied. From Tables 5 to 9 it can be seen that the total amounts of food eaten in descending order are: fish 19,032 g, *Ulva* 5,664 g, *Laminaria* 2,161 g, cabbage 1,889 g, *Macrocystis* 1,481 g, *Gigartina* 0,298 g. If the number of times a particular food was chosen out of the 30 times the food was provided is considered, the following emerges: fish 19, *Ulva* 16, cabbage 10, *Laminaria* 2, *Gigartina* and *Macrocystis* one each. The three foods most preferred are thus fish, *Ulva*, and cabbage, none of which appears regularly in the natural habitat. The three which do appear frequently on the beaches were eaten only on the first night, i.e. when the animals were starved.

It may be assumed that the location of food by *Tylos* is partly by olfactory means, as fish, *Ulva*, and cabbage all have some odour, whereas the red and brown algae are practically odourless when fresh. The second pair of antennae are extremely well developed, and it has been demonstrated in *Ligia* (Hewitt 1907), that these antennae have an olfactory function.

Second choice

As was frequently observed, *Tylos* will feed on dry brown algae even when fresh were available. This aspect was investigated by means of a preference test, done in the same way as the previous test, but using only two containers of 10 animals each. In each was placed a piece of fresh and dry alga (*Ecklonia*) of approximately equal weight. The dry alga was weighed at midday in all cases, so that the water factor would be of minimal importance. The controls show that if weighed at midday, any water taken up during the previous night was again lost by the time of weighing. The dry controls remained at almost constant weight. The percentage water loss for the fresh alga was not calculated, as the fresh alga was never eaten. From Table 10, it can be seen that after six separate feeding sessions, only the dry alga was eaten. An explanation for this preference is probably that the mucilaginous exudation of the fresh alga is too sticky for the mouthparts to cope with, and is thus avoided.

Food preferences of juvenile Tylos

As the juveniles are usually found on the debris lines, where the smaller pieces of plant and animal matter wash up, it was decided to investigate the food preferences of these forms. Two containers of 10 animals each (ranging from 8 to 20 mm) were used. The choice of food given was fish, *Ulva*, *Macrocystis*, cabbage, and *Plocamium* (a small finely divided red alga). The results of this test may be seen in Tables 11 to 14. From this it would seem that as in the adults, the juveniles have a preference for animal matter (0,650 g fish eaten) but that almost similar amounts of *Ulva* and *Plocamium* were eaten (0,305 g and 0,376 g resp.). Cabbage was seldom touched, and *Macrocystis* not at all.

STRUCTURE OF THE ALIMENTARY CANAL (See Fig. 22)

The two main references dealing with the alimentary canal of isopods are Murlin (1902) and Nicholls (1930), both of which deal with forms such as

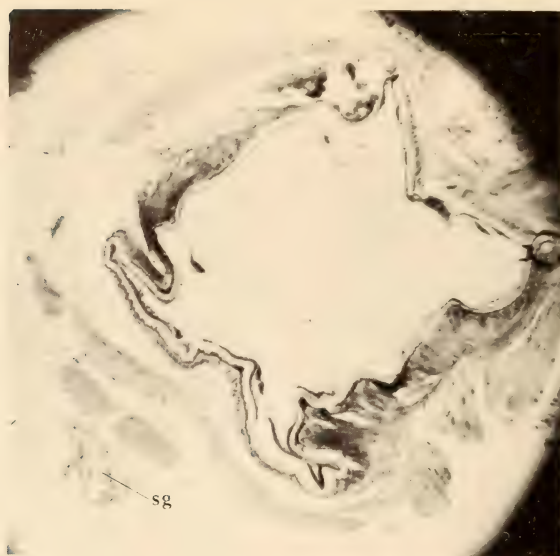


Fig. 21a.

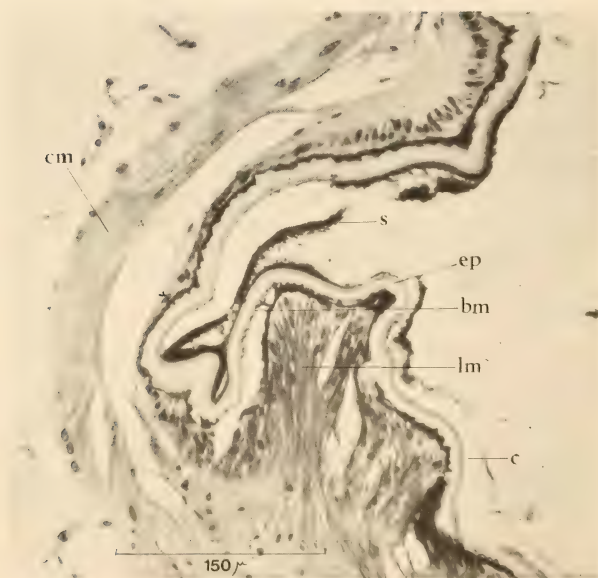


Fig. 21b.

Fig. 21. *Tylos granulatus*. a. Cross-section of oesophagus. b. Portion of wall of oesophagus; b.m.—basal membrane; c.—cuticle; c.m.—circular muscle; ep.—epithelium; l.m.—longitudinal muscle; s.—setae; s.g.—salivary gland

Ligia, *Porcellio*, *Oniscus*, and *Philoscia*. The only work dealing with *Tylos* is that of Barnard (1925) which contains a superficial description of the 'stomach' of the animal.

In general terms *Tylos* conforms with the overall isopod pattern, but has several differences, which are mentioned below in the relevant sections. The mouth is situated dorsal to the oral appendages, and just below the frontal lamina of the head. The mouthparts consist of one pair of mandibles, two pairs of maxillae, and a pair of maxillipeds. There is no obvious buccal cavity, the mouth leading directly into the short oesophagus, which together with the gastric mill constitutes the foregut. The walls of the oesophagus are strongly convoluted and are covered with very fine backwardly directed setae. Externally the oesophagus is surrounded by glandular material of the rather ill-defined salivary glands. These latter open into the oesophagus near the mouth. In cross-section (Fig. 21a, b) the oesophagus is roughly square, with the main masses of longitudinal muscles concentrated at the centres of the sides of the square. The chitinous cuticle has outgrowths in the form of numerous setae, and is secreted by a single layer of epithelial cells just beneath it. The entire oesophagus is surrounded by circular muscle fibres which tend to be arranged in large bundles. Bands of muscles stretch from the oesophagus wall to the exoskeleton of the head region, the salivary gland tissue being situated between these bands.

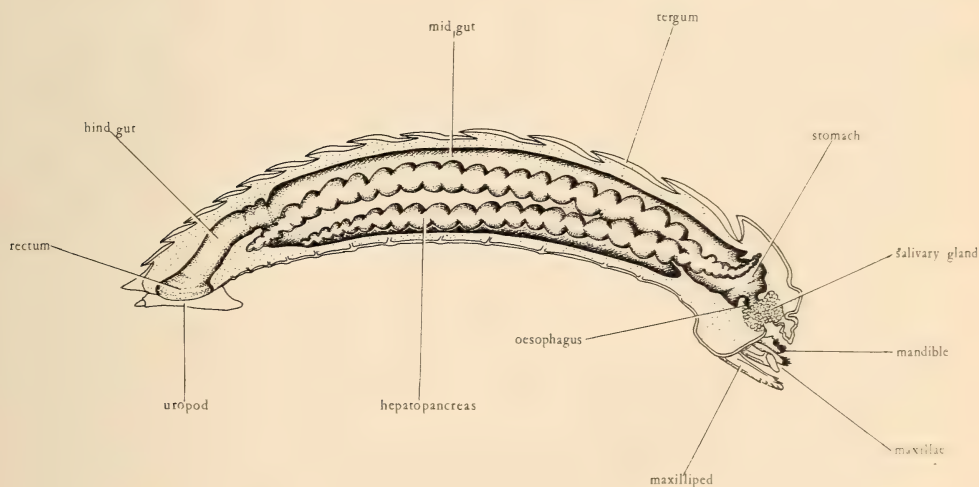


Fig. 22. *Tylos granulatus*. Lateral dissection, showing position of alimentary canal.

The oesophagus opens into the 'stomach' which contains a very efficient gastric mill (Fig. 23), made up of the following structures:

1. The lateral ampullae. These are projecting structures, the median faces of which meet above the opening of the oesophagus. These median faces have a

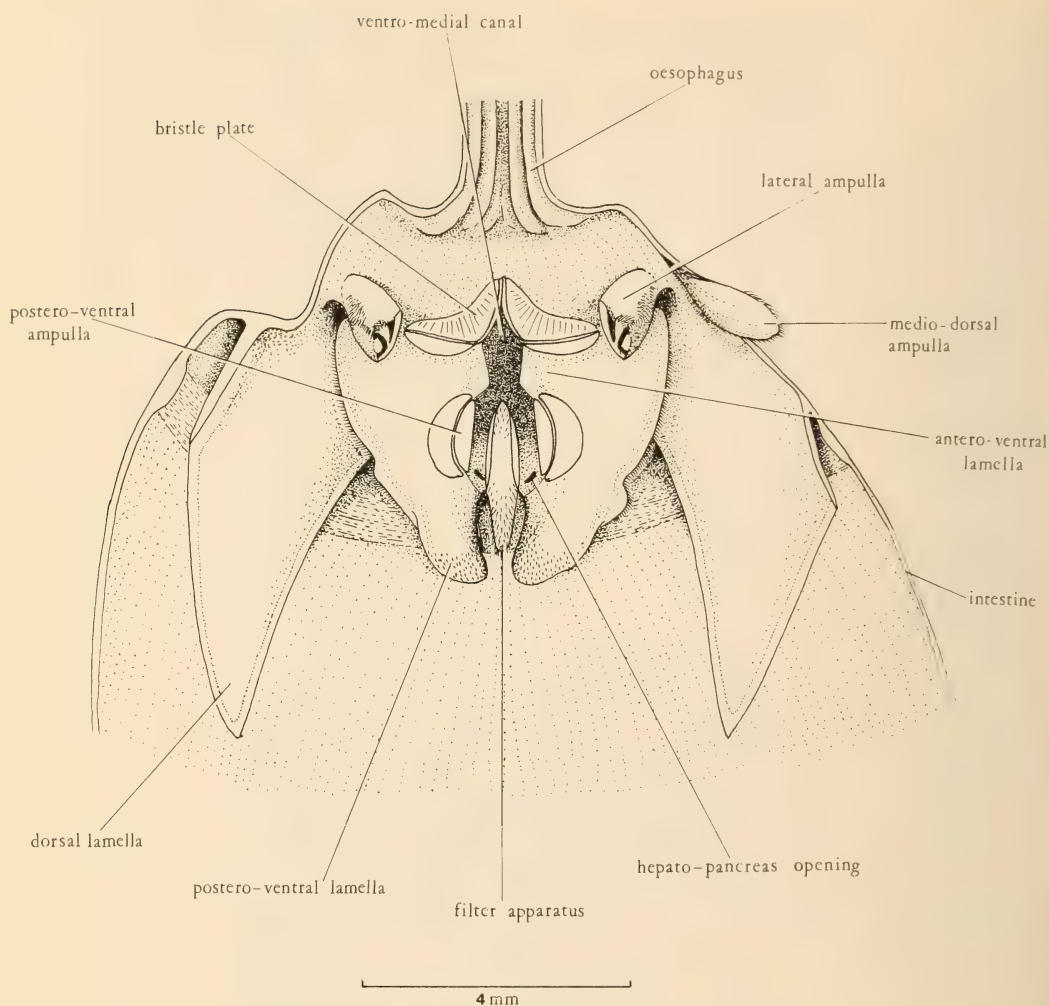


Fig. 23. *Tylos granulatus*. Structure of the 'stomach'.

trilobed chitinous structure possibly used for grinding. *Tylos* lacks the small antero-lateral ampullae found in *Ligia* and related isopods.

2. The median anterior ampulla, situated on the ascending anterior wall. This is a lobed structure fringed with setae.
3. In the floor of the foregut, below the lateral ampullae, is a pair of crescentic bristle plates, formed by the fusion of many bristles. The anterior portion of these plates meet in the midline but diverge posteriorly. Posterior to these plates are the ventral lamellae, while between them is the ventro-medial channel.

4. The ventral lamellae may be divided into an anterior and a posterior region. The anterior region, the margin of which is fringed with setae, bears on each side a pair of plates, not mentioned in the description of *Ligia* or any other isopod. These may be termed the postero-ventral ampullae. The latter have a horizontal crescentic plate, as well as a medio-vertical plate, which forms part of the wall of the ventro-medial. The posterior ventral lamellae project into the midgut in the form of two rounded lobes armed with short bristles.
5. In the ventro-medial region, just opposite the medio-vertical plates of the postero-ventral ampullae, is an elongate spindle-shaped structure, the filter apparatus. The anterior portion has a pair of lateral plates which work against the medio-vertical plates of the postero-ventral ampullae. The posterior portion projects between the lobes of the ventral lamellae, and is equipped with numerous setae. This filter apparatus divides the ventro-medial channel into two portions, each of which ends posteriorly at the opening of the hepatopancreas.
6. Situated dorso-laterally and joined along the midline are the two lobes of the dorsal lamina. These are acutely triangular in shape, consist of two layers of chitin, and project into the midgut.

The hepatopancreas

As already mentioned, the gland on each side opens into the posterior portion of the ventro-medial channel. Each gland consists of three tubular moniliform portions, two postero-lateral and one antero-lateral (Fig. 22). The postero-lateral portions stretch back along the mid- and hindgut, almost to the last segment. The short antero-lateral portion stretches obliquely upwards on either side of the 'stomach'. In section (Fig. 24) the hepatopancreas can be seen to consist of a single layer of glandular epithelial cells, around the central lumen of the gland. In places the wall of the gland appears to be more than one layer thick but this is merely due to the convolutions of the gland. The cells are elongate with a highly granular cytoplasm and large deep-staining nuclei. In the distal portion of many of the cells, large vesicles may be seen. These are probably droplets of the secretion of the cells. In addition, many of the cells have large clear central vacuoles. The outer surface of the hepatopancreas has a very thin layer of connective tissue, between which and the glandular cells, very thin circular muscle fibres may be seen. This muscle layer may be continuous but is difficult to assess, being very thin.

The midgut

The gastric mill ends at about the level of the first thoracic segment and opens into the capacious midgut, which stretches back to meet the hindgut at the level of the tenth segment. There is no trace of a typhlosole, as found in *Ligia*. In cross-section (Fig. 25) it can be seen that the midgut is lined with a very fine chitinous intima, in which there is no sign of holes or ostia. Murlin

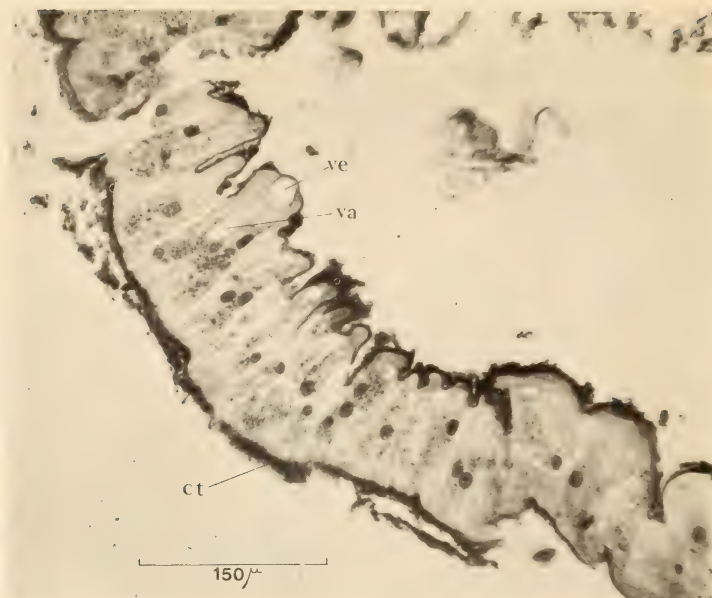


Fig. 24. *Tylos granulatus*. Cross-section of hepatopancreas; c.—connective tissue; n.—nucleus; va.—vacuole; ve.—vesicle

(1902) mentions the presence of very fine pores in the intima of the midgut of several terrestrial isopods, including *Oniscus* and *Asellota*. Nicholls (1930) could not find these holes in *Ligia*, neither were they present in *Armidillidium*, *Porcellio*, or *Idotea* (McMurrich 1896). Beneath the intima is a single layer of elongate epithelial cells. These are large cells, about 150 μ in length, and have large deep-staining nuclei. These epithelial cells are remarkable for their large vacuoles surrounded by a thin granular cytoplasm. Numerous granules are visible in this cytoplasm, as well as minute droplets. These may be absorbed digestive products. The outer bases of the epithelial cells are surrounded by a very fine basal membrane. The outermost layer consists of a sheath of connective tissue, with separate bundles of oblique muscle fibres.

The hindgut

The midgut opens into the hindgut at a constriction. The hindgut which forms about one-quarter of the total gut length, occupies the last four segments and opens at the anus, which is covered by the valve-like uropods. The innermost layer of the hindgut is a very fine chitinous intima, beneath which is found a single layer of elongate epithelial cells, similar to those of the midgut (Fig. 26). These cells contain large vacuoles, but not as obvious as those of the midgut. The cytoplasm does not have many inclusions. The epithelial layer is very convoluted, with connective tissue between it and the next muscle layer. The muscu-

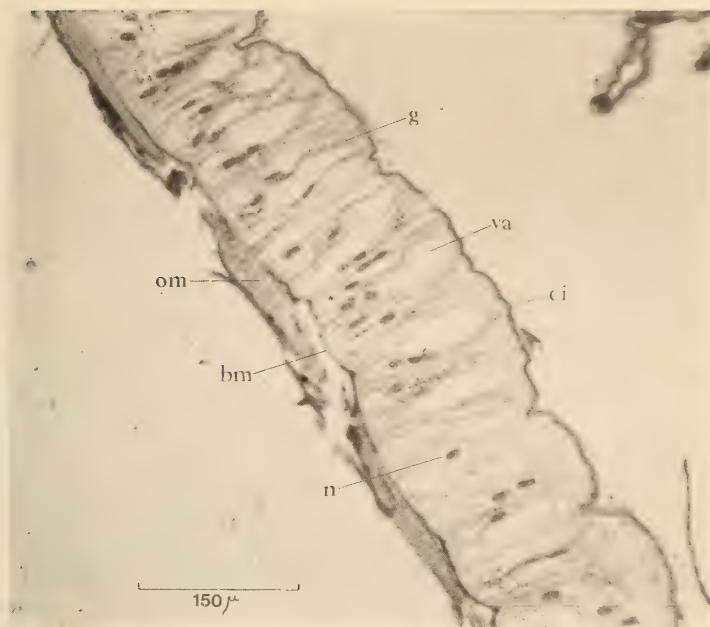


Fig. 25. *Tylos granulatus*. Cross-section of midgut; b.m.—basal membrane; c.i.—chitinous intima; g.—granules; n.—nucleus; o.m.—oblique muscles; va.—vacuole

lar sheath surrounding the hindgut consists as circular as well as longitudinal fibres. The circular fibres form a continuous band around the gut, while the longitudinal fibres are arranged in separate bundles on the circular muscle band.

THE PROCESS OF DIGESTION

The progress of food through the gut involves several stages, some being not particularly clear. The food is manipulated and eventually cut up by the mandibles, then passes into the oesophagus in the form of fairly uniform pieces. The posteriorly directed setae of the oral region all assist the food in moving into the oesophagus, and prevent it from slipping out. The fine hairs of the oesophagus have a similar function. While passing into the oesophagus the food is mixed with the secretion of the salivary glands. (The exact nature of these secretions is uncertain, as very refined techniques are needed to collect and test them. A certain amount of mucilaginous fluid is secreted.) Contraction of the muscles of the oesophagus walls passes the food on to the gastric mill. As none of the structures of this complex is particularly hard, it would seem unlikely that any trituration occurs. Rather it would seem that the lateral ampullae by muscular action force the food against the bristle plates. Similarly the postero-ventral ampullae would work against the filter apparatus, again squeezing the food. Both these actions would result in food plus tiny pieces in suspension, to pass



Fig. 26. *Tylos granulatus*. Cross-section of hindgut; c.i.—chitinous intima; c.m.—circular muscles; l.m.—longitudinal muscles

into the ventro-medial channel. Contraction of the hepatopancreas would force its contents into this channel, to be mixed with the food-fluid, and allow the enzymes present in the secretion to act. Large food particles would be prevented from entering the channel by the posteriorly directed setae and allow the food to pass only backwards into the midgut.

The site of absorption has been the subject of much controversy. It has been shown that in *Nephrops* (Vonk 1960), absorption can and does take place in the midgut. Several decapod crustaceans, including *Astacus* (Jordan 1929), *Nephrops* (Yonge 1924) and *Atya* (Van Weel 1955), have been shown to absorb substances through the hepatopancreas. Nicholls (1930) showed that in *Ligia* absorption took place through the midgut (even though lined with chitin) and also through the hepatopancreas. It is likely that a similar set-up occurs in *Tylos*. With contraction of the hepatopancreas the secretions are forced into the ventro-medial channel, and mixed with the fluid part of the food. Any excess secretion is forced into the upper portion of the gastric mill and mixed with the solid food. With relaxation of the hepatopancreas, the mixture of foods in the channel is drawn into the lumen of the gland. Dissolved food in the form of monosaccharides and amino acids may then be absorbed by the glandular epithelium. Oil droplets are probably also taken up, as is known to occur in *Atya* (Van Weel 1955). Contraction of the muscles of the gastric mill then forces

the solid food particles and hepatopancreas fluid into the midgut where a longer process of digestion takes place, and the released substances absorbed through the chitinous intima of the gut (Vonk 1960). Food is probably kept in the midgut for a period of up to 48 hours, depending on the type of food. Observation shows that an adult *Tylos* having fed on *Ecklonia* does not feed on the following night, and probably will not feed on the second night either. The 'storing' of the food probably accounts for the sporadic emergence of the adults. If the midgut is full of digesting food, there would be no need to emerge and feed.

The secretion of the hepatopancreas

From a perusal of the food list, it will be seen that *Tylos* is omnivorous, with a bias towards algae. Omnivorous invertebrates almost invariably possess all three major types of digestive enzymes, viz. carbohydrases, proteases, and lipases. With this in mind, simple qualitative tests were performed to establish the presence of these enzyme types in *Tylos*.

A homogenate of hepatopancreas gland was prepared in the following way. The glands of 40 animals were removed, weighed, and homogenized with a phosphate buffer of pH 7.0. The homogenate was then centrifuged and the supernatant further diluted with buffer to give a 10% homogenate solution.

Carbohydrases: tests were performed for three carbohydrases, cellulase, amylase, and sucrase. In the case of cellulase, a positive control in the form of homogenate of *Helix* midgut was used, as well as a negative control in the form of boiled hepatopancreas homogenate. No cellulolytic activity could be detected in the active *Tylos* homogenate and it was concluded that no cellulase was present. Amylase was tested for by means of starch solutions and Fehling's test for reducing sugar. The latter test was positive, indicating the presence of some amylase-type enzyme. Sucrase was tested for, a positive control in the form of invertase solution being used. A positive Fehling's test indicated the presence of a sucrase-type enzyme.

Lipase was tested for by means of the action of the homogenate on milk, phenolphthalein and NaOH being used as indicators. Fatty acids were released indicating the action of a lipase.

Protease was tested for by the use of congo red fibrin at pH 7.0. Only after 48 hours did any red coloration appear in the experimental tube, indicating that some fibrin has been digested to release the red particles. The test was repeated using a phosphate buffer of pH 8.0. After two hours the experimental tube contents became red. In both tests, a dilute solution of trypsin was used for comparative purposes. It was concluded that some protease was present which operated in the alkaline range.

The results of the test for protease seemed to suggest that the pH of the gut must vary if all the enzymes are to function close to their optimal pH. Several animals were opened and the pH of the gut tested directly. The results of this showed that whereas the pH of the hepatopancreas was 6.3, that of the gastric mill and anterior part of the midgut is 6.9, while the posterior midgut has

a pH of 7.4, and the hindgut 6.8. It would seem that the carbohydrases have maximum activity in the foregut and anterior midgut, while the posterior midgut with its higher pH would be the centre of protease activity. The acid pH of the hindgut is probably due to the start of decomposition. The results are similar to those obtained by Nicholls (1930) for *Ligia oceanica*. He found the pH of the hepatopancreas to be in the region of 6.1–6.3, with the pH of the gut usually higher than that of the gland. The pH of the intestine varied from 6.2 to 7.2, while the rectum had an acid pH of 6.0.

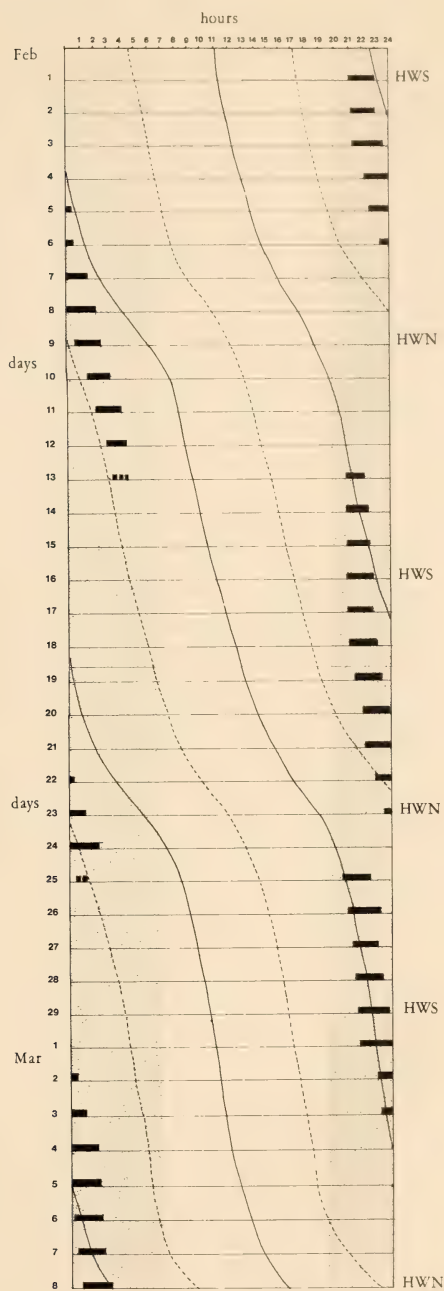
RHYTHMICITY

In an attempt to gain more precise information regarding the rhythmic activity of *Tylos*, uninterrupted nightly observations were done on *T. granulatus* for 36 consecutive days. Consecutive observations over a long period were not carried out for *T. capensis*; interrupted observations over several weeks were nevertheless made. So as to get an overall view of the situation, and to see trends in the rhythm, all the information for *T. granulatus* was presented graphically, together with other relevant factors. With reference to Figure 27, the following should be noted.

1. The horizontal axis denotes the 24 hours of the solar day.
2. The vertical axis denotes consecutive days, the actual dates being given.
3. Solid black horizontal lines represent the time emerged by the animals.
4. Stippled areas denote dark of the sun, i.e. night.
5. Curved solid lines indicate low tide, the actual time of low tide being where the line intersects the horizontal day line.
6. Curved broken lines represent high tide, the actual time of high tide being where the line intersects the horizontal day line.
7. As the animals emerge and return over a period of up to 30 minutes, actual time of emergence was taken when at least ten animals could be seen emerging simultaneously. Similarly, time of return was taken when at least ten animals could be seen returning.

Discussion of Table 15 and Figure 27

From the above data several facts emerge, some of which can be explained and others which can only be speculated about. The most obvious fact is that *T. granulatus* is purely nocturnal and usually emerged at least one hour after sunset. (*T. latreillei* by contrast is a diurnal animal, preferring damp shady crevices of rocks. Pardi (1955) made use of this fact when investigating the orientation mechanism of this animal.) The shortest time observed between sunset and emergence was one hour. The shortest time observed between return into the sand and sunrise was $2\frac{1}{2}$ hours. The mean time emerged for the 36 consecutive days of observation was 2.1 hours, the mode 2.0 hours. The longest time out was about $2\frac{1}{2}$ hours while the shortest time out (apart from the exceptional

Fig. 27. Rhythmic activity of *Tylos granulatus*.

13th and 25th) was $1\frac{1}{2}$ hours. The time the animals have to feed is thus very short, and appears to be strictly controlled.

It can be seen that there is an overall trend to emerge later each night; this gap between the time of emerging for successive days may be anything from 0 to $1\frac{1}{2}$ hours. Occasionally the animals emerge at about the same time for several consecutive nights, e.g. from the 14th to the 18th inclusive. If the time for re-entry for these days is noted, however, it can be seen that this becomes later each day. If the time between re-entry is plotted against successive days, it can be seen that a line may be drawn through these points at the 24,5 level. This is the mean of the times between re-entry. The mode of this time gap, however, is 24,7 hours. Excepting the unusual days of the 13th and the 25th, the time between re-entry on successive days is always more than 24 hours. If the cycle is one of 24,8 hours which is not unusual for littoral animals, there should be a correlation between the time of emergence of the animals and the time of low tide (or the time of high tide). With this in view, Spearman's Rank Correlation Test was done, using the three sets of consecutive 12-day observations and ignoring the days in between. This test gave positive correlations of 1,0, 0,84, and 0,9. The significance of this correlation was tested, using the 't' test, which showed that the probability of this correlation occurring by chance was less than 0,01, i.e. there is a positive correlation between the time of low tide and the time of emergence. It must be noted that although this test shows positive correlation between tides and the cycles of activity, this does not imply a causative connection between these phenomena. It can be stated with considerable certainty that *T. granulatus* possesses a 24,8 hour (lunar day) rhythm.

An explanation for the consecutive days on which the animals emerge at the same time, may be that not all the same animals emerge, thus each day some animals emerge later than others, and return to the sand later each day. Brown (personal communication) states that in some sandy beach animals which burrow, only part of the population emerges each day. Thus in the mollusc *Bullia digitalis* it has been estimated that only 12% of the population emerges at any one tidal cycle.

If the times for re-entry and emergence are examined against the times of high and low tide, it is seen that on five days out of the 36 the animals emerged near the time of high tide, but only during neap tides. On all the other days they emerge either at low tide, or during ebb tide. It is obviously advantageous to the animals to emerge during a receding tide. If they emerged close to the time of high tide, there exists the possibility of being swept to sea.

As has been shown, *Tylos* has under natural conditions a lunar day rhythm. It thus emerges a little later each night. If this system were invariable, eventually it would not emerge until dawn. Being purely nocturnal, as already stated, this would be most unsuitable. The animals correct for this effect of the lunar day rhythm by a 'switch back' once a certain stage of the cycle is reached. This switch back takes it to the early evening hours after sunset which then allows many days of uninterrupted lunar rhythm. This switch back was seen to operate

on the 13th and on the 25th. On the former day a few animals were seen to emerge at about 0300 hours, just on high tide. A vast number emerged at 2045 hours, whereas on the previous day the majority emerged at 0250 hours. It was obviously important not to emerge at 0300 hours on the 13th, i.e. at high tide, as the tides were approaching springs. The animals would be low down on the beach, and the increasing height of the high tide would certainly endanger them. Emerging at 2045 hours brought them out at low tide when it was quite safe for feeding.

Twelve days later, the animals again switched back. A few emerged at 0015 on the 25th, but a great number came out at 2030 hours. Again the tide was approaching springs and although on the 23rd and 24th they had emerged at high tide, the tide was getting higher each day, rendering their late emergence more dangerous. To cause this switch back, there must be some rhythm imposed on the lunar day rhythm. In all probability this is a semi-lunar or 14-day rhythm. This would keep the animals in phase with the spring tides, the period between successive springs being 14–15 days. The fact that the switch back of the 25th occurred only 12 days after the previous one does not disprove this, but may represent an abnormality in the rhythm due to external factors. It is interesting to note that in both the observed switch backs, these occurred four days before the spring tide. That the rhythm is a 15-day one may be inferred if Figure 27 is examined. Twelve days elapsed between the start of observations on 1 February, and the switch back of the 13th. The HWS occurred on the 1st. Three or four days before this the animals would have switched back, i.e. on 28 January. Further evidence for this is that on 28 January the animals were observed to emerge at 2100 hours at Lambert's Bay, 288 km up the coast. (As there are only three 15-day cycles available, statistical verification is not possible. With a minimum of six cycles, 90 days of observations would need to be done.)

As it has been shown that *Tylos* possesses a 24.8 hour rhythm as well as possibly a 15-day rhythm, it remains to investigate whether these are inherent or whether they are triggered by external factors. With this in view, a rather unrefined experiment was performed. A population of 25 animals of *T. granulatus* was placed in a perspex/glassfibre container, having an area of 250 cm² and a depth of one metre. This container was placed in a completely dark room, having a temperature of 17°C, and a range of about 3°C. This room was kept in constant darkness for 18 days. The only light was that of a torch used for brief intervals for observation. Food in the form of moist *Macrocystis* and *Ecklonia* was regularly provided so as not to be a limiting factor. The sand used at the start was damp, and at irregular intervals small amounts of sea water were added to prevent drying out.

The animals were left for two days to acclimatize before observations were started. The animals in the darkroom were thus separated from the effects of the tides, temperature fluctuations, and illumination affecting the animals on the beach, which were used as controls. The emergence of the animals from both the beach and the darkroom was plotted against a time axis (Fig. 28). At the

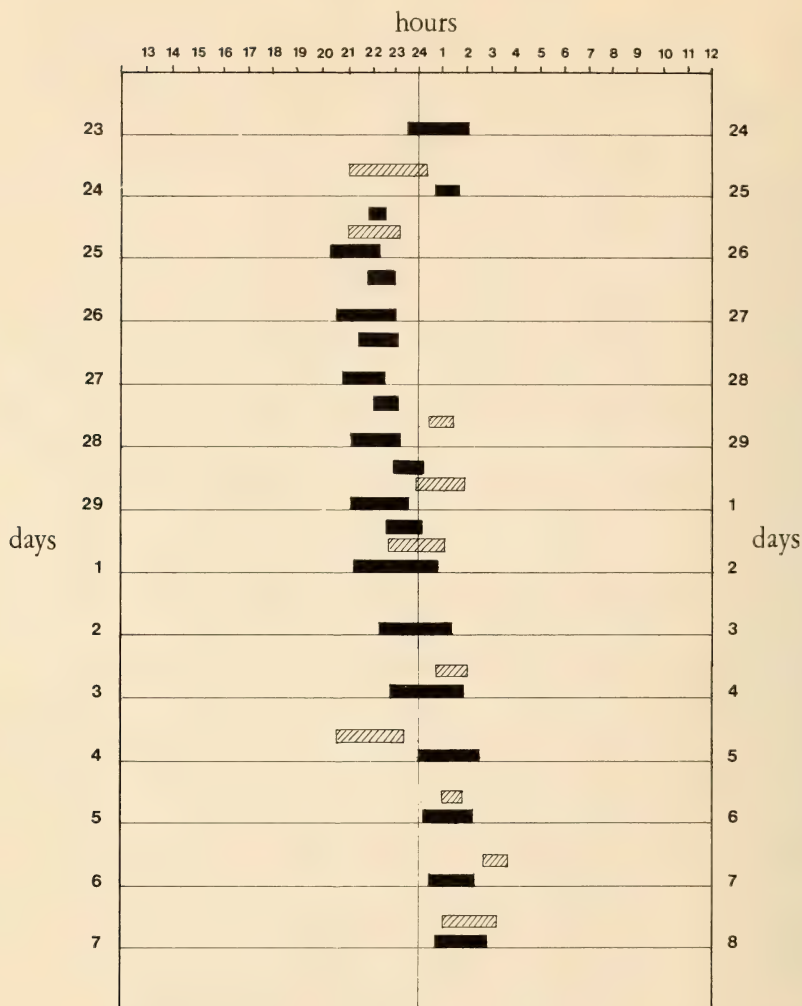


Fig. 28. Rhythmic activity of *Tylos granulatus*.

same time, ten animals were kept in a container of sand, away from the beach but under normal light and temperature conditions. These latter could unfortunately only be observed for six days. These results are also plotted on Figure 28. On the 29th, after it was suspected that not all the same animals emerge each night, the darkroom animals were marked with numbers painted on their dorsal surfaces so as to record in greater detail the exact animals which were emerging. (Marking animals on the beach is not practicable; the number feeding on 0,2 m² of kelp was often found to be over 300. A very rough estimate of the number of animals in the study area at Blouberg is between 3 000 and 4 000.)

The results of these observations may be seen in Table 16. From the latter and from Figure 28, the following observations were made:

1. For the period of observation, the experimental animals emerged only during night hours, even though they were subjected to constant darkness.
2. The same animals do not necessarily emerge every night, and on some nights none emerge.

It was found that on 22 March, 29 days after the experimental animals had been placed in the darkroom, nine emerged at 1700 hours, i.e. two hours before sunset. The rhythm which kept the animals nocturnal appeared to be breaking down. The container with the animals was then placed in the open where they received normal light and temperature conditions. The following day the animals emerged at about 2100 hours, almost two hours after sunset. They had thus corrected the time of emergence, once normal light conditions were restored. It is interesting to note that the Blouberg population emerged at 2015 hours on the same day.

Discussion of Table 17 (Tylos capensis)

Even from the limited data available for observations on *T. capensis*, several facts may be deduced. As in *T. granulatus* the present species is strictly nocturnal and usually emerges at least one hour after sunset. The time of emergence is again usually close to that of low tide, as in *T. granulatus*, while the actual time emerged is from $1\frac{1}{4}$ to $2\frac{1}{2}$ hours. Thus a lunar day cycle of 24.8 hours may be inferred for this species. As the animals always emerged at or around the low tide of the dark hours, and as the observations cover a period of almost $2\frac{1}{2}$ months, it may also be inferred that the switch back mechanism, controlled by a 15-day cycle is present in this species.

REPRODUCTION AND GROWTH

Reproduction in *Tylos* is geared to the littoral and almost terrestrial mode of life. Spermatozoa must be transferred to the female without the assistance of water. For this, the male is provided with copulatory stylets. These latter are adaptations of the endopods of the second pair of pleopods. The basal portion of each stylet lies parallel with the posterior margin of the last pereion segment. At the midline, each stylet is bent at a right angle posteriorly. In the adult male of *T. granulatus* this portion can be 3–4 mm in length, and is adpressed to its opposite member. Each is concave on the inner face, the two together forming a channel for the passage of the spermatozoa. (The presence of the stylets, which begin to develop in the very small males, is useful in distinguishing the sexes.) The spermatozoa are produced in the testes, three on each side, situated in segments three and four, dorso-lateral to the gut, and are passed into the stout vasa deferentia. In these the needle-like spermatozoa are clustered into spermatohores. The male genital orifice on pereion segment seven is just opposite

the bend in the copulatory stylets, and the spermatophores pass along this channel to be transferred to the female. The actual transfer was never witnessed, and could have taken place at the surface or beneath the sand. Many of the males dissected from almost all the localities were found to have spermatozoa in the vasa deferentia. The ovaries during the breeding season are large sac-like organs stretching between segments two and eight and are situated above the hepatopancreas. A short oviduct leads ventrally to the female genital orifice which is situated at the base of the fifth pereopods. Oostegites which form the brood pouch for the eggs are not present in all the females. These presumably appear after a moult, when the female has ripening eggs in the ovaries. Ovigerous females of *T. granulatus* were found during January and February from several localities. The minimum length of an ovigerous female is 36 mm, the maximum length found, 41 mm. Up to 1969, two ovigerous females of *T. granulatus* were known, from the mouth of the Schuster's River, collected in February 1937. Numerous ovigerous females have now been collected. The eggs are 1,6–1,8 mm in diameter. Barnard (1940), writing about the first two ovigerous females, states that the oostegites remain flat and that the brood pushes the sternum upwards. This was found to be true in all the later specimens. Barnard mentions that this forcing up of the sternum results in a degeneration of the females' internal organs, and he concludes 'In fact it would seem improbable that the mother could recover after the escape of the brood' (1940: 438). With this in mind, ovigerous females were injected with formalin on capture. When dissected, the alimentary canal and heart were found to be normal, only the ovaries being degenerate. It would seem probable that Barnard's conclusions were the result of imperfect preservation.

Of *T. capensis*, this is the first record of ovigerous females; several were collected from Strandfontein from November to January. The minimum length of an ovigerous female is 20 mm.

From the beginning of September (in *T. capensis*) and the beginning of October (in *T. granulatus*) the ovaries start to enlarge and egg formation commences, even before oostegites become apparent. By the end of January (*T. capensis*) or the end of February (*T. granulatus*) ovigerous females are no longer encountered. In both species it was noted that ovigerous females were only found above the high tide zone, up to 20 metres in *T. capensis*. This is probably connected with incubation of the eggs, as the sand above the high tide mark has a fairly constant and slightly higher temperature than the sand lower down the beach which is influenced by the temperature of the incoming tide.

Measurements of many individuals of *T. granulatus* and *T. capensis* from Blouberg and Strandfontein respectively, if plotted in the form of histograms (Figs 29, 30), show that there are at least four moults and possibly more in the life history of the animals. Figure 29 clearly shows four peaks of size, and if the ecdysis for the very small individuals in the brood pouch is added it seems probable that there are five moults, and that only in the final one do oostegites appear in the females.

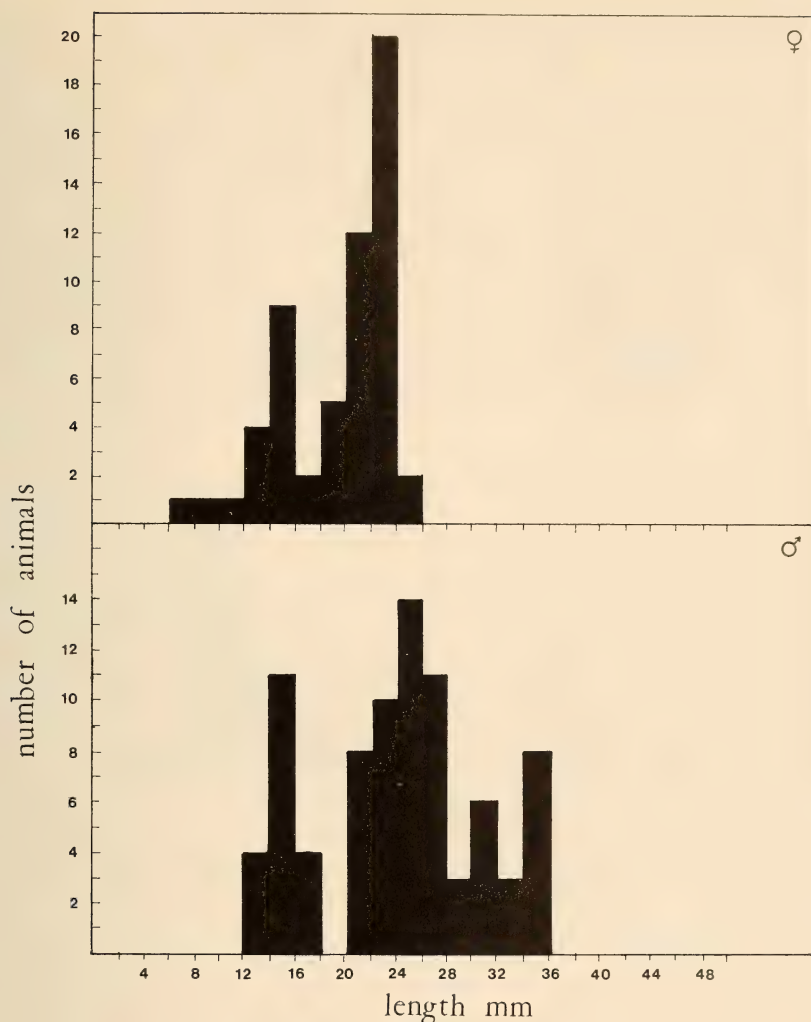


Fig. 29. *Tylos granulatus*. Histogram showing size grouping of males and females.

ASSOCIATION OF *TYLOS* WITH OTHER SPECIES

Tylos granulatus

As a nocturnal inhabitant of sandy beaches, this species would seem at first to have very little contact with other animals. On closer examination a few associations emerge, but one important factor remains unexplained. After more than two years of observation, no predator has been recorded. In the sand itself, the only possible predators could be golden moles (*Chrysochloris capensis*) which occasionally burrow along the upper beaches. Birds such as gulls (*Larus* spp.) and cormorants (*Phalacrocorax* sp.) are active during the day when the

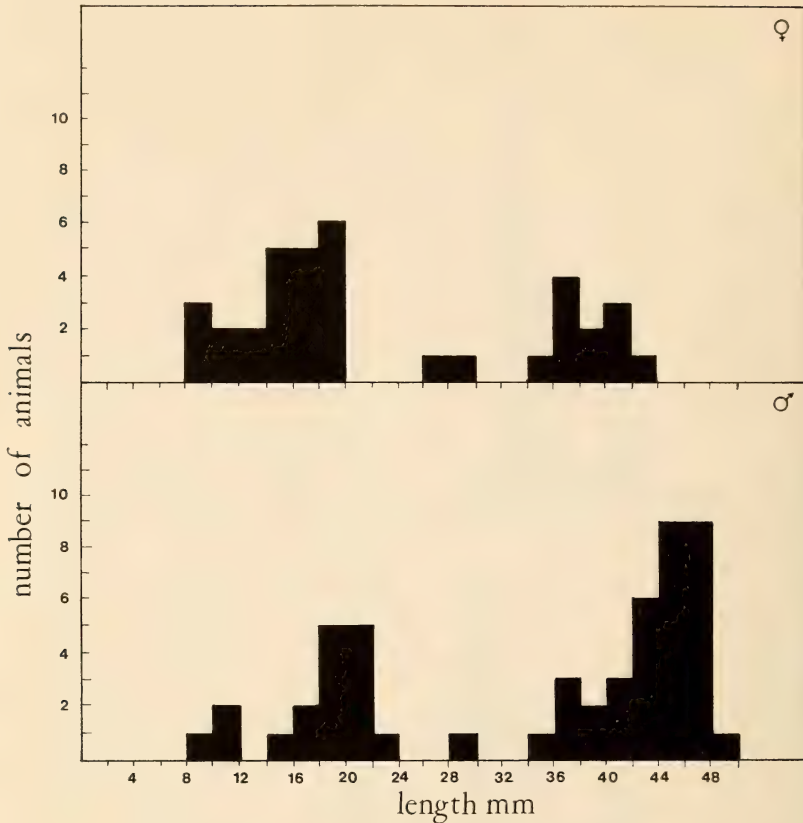


Fig. 30. *Tylos capensis*. Histogram showing size grouping of males and females.

isopods are up to 400 mm beneath the sand. Even probing in the sand is unlikely to expose any animals. It is perhaps possible that genets (*Genetta* sp.) and polecats (*Ictonyx* sp.) from the surrounding bush could prey on the animals at night. This is, however, pure speculation, no proof having been found. Perhaps this species does not have any predators at all.

COMPETITORS

Apart from the competition for space in the sand, and for food amongst the individuals of the species itself, only two food competitors have been observed. These are the amphipod *Talorchestia quadrispinosa* and the carabid beetle *Platychila pallida*. *Talorchestia* is often seen in great numbers around decomposing kelp, but even in great numbers these animals represent a rather unimportant competitive element, when compared with the amount of algae eaten by the isopods. *Platychila* is a well known member of the sandy beach community, and has a distribution very similar to that of *T. granulatus*. This

pale beetle is about 20 mm in length, and is also nocturnal. These insects were often encountered about 150 mm below the surface of the sand when digging for *Tylos*. At night they were often seen scampering over the sand. Possessing relatively large mandibles, they are predacious, and although never seen actually eating *Tylos*, they were often seen feeding alongside the juvenile isopods on the debris lines. They were seen to feed on *Physalia* and other animal matter, and thus represent a fairly important competitive element low down on the beach where only the juvenile *Tylos* feed. Another carabid beetle often found in the sand with *Tylos* is *Acanthoscelis ruficornis*. Also a predator, fewer of these were found than of the previous beetle. *Pachyphalaria capensis*, a tenebrionid beetle, is often found with *Tylos*, scavenging mainly on algae, but does not occur in sufficient numbers to constitute an important competitor.

COMMENSALS

Barnard (1932: 218) noted the following, when dealing with *T. granulatus*: 'A minute oligochaete lives among the pleopods. It is 2.5–3.0 mm in length, whitish, with 4 bundles of straight and apically simple spines in each segment usually 3 spines in each bundle. It may be termed *Enchytraeus tylidus* n.sp.' Many specimens of this oligochaete were found on animals from all the localities listed. Samples of 10 adults and 10 juveniles (less than 20 mm in length) from Blouberg and Lambert's Bay were examined. The results are given in Table 18. From this it can be seen that almost all the adults carry these commensals, and that the juveniles are 'infected' only after they have reached a length of about 20 mm. The worm may breed beneath the pleopods as structures resembling egg cases have been found. On further investigation it was found that since Barnard's mention of the worm, it has passed unnoticed and has never appeared in the *Zoological Record*. The oligochaete has been found only on *T. granulatus* and is probably an obligative commensal, confined to this single species.

Another commensal was a tiny mite which was sometimes found between the pleopods, but more usually beneath the extensions of the fifth abdominal segment and beneath the uropods in the region of the anus, where the exoskeleton is relatively thin. No visible damage due to the commensal could be seen in any of the animals examined. From one to four mites may be present per isopod; of 25 examined, 9 carried the mites. Dr G. C. Loots (personal communication) states that the mite is an undescribed species of the genus *Veigaia*. He also notes that the members of this family usually play a predatory role in micro-habitats, especially in rich soil. This is the first record of a member of the family having been found commensal on an invertebrate. Dr Loots suggests that the mites may feed on the faeces of the isopod; this would account for their concentration in the pleon region.

Tylos capensis

As with the former species, no predator has been found for this species.

The beetles *Acanthoscelis ruficornis*, *Platychila pallida* and *Pachyphalaria capensis* have all been found in association with *T. capensis* in False Bay.

COMMENSALS

Mites of the same species of *Veigaia* as were found on the former species of *Tylos* were collected from specimens from Strandfontein, Breë River, and Knysna. 11% of the Knysna isopods, 8% of the Breë River, and 5% of the Strandfontein animals carried the mites.

Also found on *T. capensis* were the third larval stage of some rhabditiform nematode, but only from the Strandfontein population. The minute worms were found in numbers of up to 100 per individual, between the pleopods, and caused no apparent damage. Hyman (1951) notes that many of these nematodes are organic detritus feeders, sometimes epizootic on invertebrates.

COMPARISON OF SPECIES AND DISCUSSION

From the present study it is apparent that the two species are very similar both structurally and with regard to their behaviour. The most obvious difference is that of distribution, *T. granulatus* being strictly west coast, *T. capensis* strictly east coast, with no overlap. The difference in sea temperatures for the east and west coasts undoubtedly has an effect on the temperature of the intertidal area. The higher sea temperature of the east coast may account for the earlier breeding season of *T. capensis*. There are also obvious differences in the size of the adults of the species, ovigerous females of *T. granulatus* being almost twice the length of those of *T. capensis*. Structurally the difference between the species is small, and lies in the degree of granulation of the exoskeleton, and the development of the ventral processes of the fifth pleon segment. Other differences which have been noted are in the choice of beach and in the depth to which the adults burrow. *T. granulatus* is found only on exposed beaches and burrows to a depth of up to 400 mm, whereas *T. capensis* only goes down to about 300 mm, and may be found on both exposed as well as sheltered beaches.

Judging from the numbers especially in *T. granulatus*, this genus is very well adapted to its ecological environment. This latter—the sandy beach, poses several problems to its inhabitants involving wave action, stability of the substrate, food supply, predators, temperature/light/humidity fluctuations, tidal rhythms. By being nocturnal and by burrowing into the sand, the animals have simultaneously solved several of these problems. There are no predators on the beach at night, whereas if the animals emerged during the day they would be vulnerable (particularly the juveniles) to being preyed on by sea birds. In spite of the relatively large surface-temperature and humidity fluctuations, beneath the sand these factors remain relatively constant. Emergence at night ensures that the temperature of the surface has dropped, thereby reducing the danger of desiccation. This latter factor is also reduced as the relative humidity increases at night. Burrowing also reduces the risk of exposure to wave action.

The most important adaptation of *Tylos* is its possession of lunar rhythms. By manifesting a lunar-day rhythm closely correlated with the time of low tide, and by being nocturnal, the animals emerge during the nocturnal low tide. This gives protection from wave action. Food in the form of organic debris is washed ashore with the high tide and left stranded at the ebb. The animals can thus feed quite safely. By restricting the time of feeding to two hours, a limit is placed on the amount capable of being eaten. This is compensated for in several ways. As the animals burrow at or near the high tide mark, the time spent in searching for food is reduced. Being omnivorous and possessing all the major types of digestive enzymes, there is no great need to be very selective with regard to the type of food. The mouthparts are very efficient and the gut capacious, thus a maximum amount of food may be eaten in the time available.

The possession of a semi-lunar rhythm ensures that the animals are kept in phase with the spring tides. In this way animals may emerge on a rising tide during neaps, but never during springs. Once again the danger of being swept to sea is eliminated. To what extent the external environmental factors influence the rhythms, and to what degree they are endogenous, is difficult to assess. That the rhythms are to some extent endogenous, is demonstrated by the fact that they continue to function under constant darkness, away from the sea. Temperature would appear to have little if any influence on the rhythm. This is necessary, for, to quote Brown (1959: 1539): 'To possess adaptive significance for the organism, a considerable degree of temperature independence is needed to permit the cycles to retain their normal lengths when exposed to the natural temperature fluctuations.' It has been shown that *Uca* and *Cambarus* retain their rhythm under constant temperatures ranging from 6 to 26°C. Temperatures within two or three degrees of freezing point, however, are capable of inhibiting the rhythm, through a slowing down of the metabolic rate. Brown (1961) introduces another factor which has bearing on the maintenance of rhythm. In *Uca*, animals which are kept together in the laboratory under constant conditions exhibit rhythms with precision, but if kept separately in individual containers, they show a gradually decreasing amplitude in their rhythms. Once a separated individual is joined by another, the rhythm is restored. This social factor has not been further investigated, and remains largely unexplained. It is likely that this has some bearing on the problem of *Tylos* where, on the beach under natural conditions, the rhythms are fairly precise and are exhibited by the population as a whole rather than by the individuals, but in the laboratory where only a small portion of the population is studied, the rhythms are subject to greater variation. External light must have some controlling and supplementing effect on the rhythms involved. Thus if low tide is close to sunset, the animals would come to the surface, and only if the light intensity is low enough will they emerge. This testing of the light intensity is probably the function of the pause observed in all emerging animals. In this connection it was noted that the animals seldom emerged at the time of full moon.

The possibility also exists that the rhythms are not endogenous, and that

under so-called 'constant' conditions, animals such as *Uca* are still responding to some less obvious external factor. It would seem from preliminary work carried out by Brown and his co-workers that this external factor may be correlated with barometric pressure, but is not this pressure itself.

SUMMARY

1. An introductory ecological/biological study of *Tylos granulatus* and *Tylos capensis* has been carried out.
2. Complete descriptions and synonymies for both species have been given.
3. The geographical distribution of *T. granulatus* was established as being from Cape Point to northern South West Africa, while that of *T. capensis* was from False Bay to southern Natal.
4. It was found that both species inhabit sandy beaches of varying slope, and sand of varying grain size.
5. Both species burrow in the sand around the high tide mark, moving up or down the beach as the height of the high tide moves.
6. *T. granulatus* was found to burrow to a depth of about 400 mm, *T. capensis* to a depth of about 300 mm.
7. Both species execute a helix-shaped path through the sand.
8. Entry point into the sand is marked by a low mound of sand, exit by a shallow hole.
9. Both species were found to be omnivorous, with a leaning towards an algal diet in the adult stage.
10. Food preference tests indicated that the adults and juveniles preferred animal matter to vegetable matter, and that the adults preferred dry algae to fresh.
11. The structure of the alimentary canal and associated structures were investigated, as well as the process of digestion.
12. Both species were found to be strictly nocturnal.
13. The rhythmic activity of both species was investigated. Both were found to possess a lunar-day rhythm, bringing them out of the sand at or close to low tide.
14. A semi-lunar rhythm is postulated. This would account for a switch back observed in the times of emergence. This mechanism militates against the animals' emerging at the time of high water of spring tide.
15. Oviposition and release of young was found to take place in midsummer, i.e. December to February.
16. Five moults are thought to occur during the animals' life span.
17. No predators were found for either species.
18. No important food competitors were found.
19. Both species were found to carry up to five specimens of a commensal mite per isopod.
20. *T. granulatus* adults were often found to have several specimens of a commensal oligochaete amongst the pleopods.

21. *T. capensis* from Strandfontein was found to carry rhabditiform nematode larvae amongst the pleopods.

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TABLE 1

Collecting localities for *Tylos granulatus*

B.K. = present author	U.C.T. = University of Cape Town
Locality	Collector
Ventura wreck site, S.W.A.	B.K.
Möwe Point, S.W.A.	B.K.
Anichab, S.W.A.	Panning, B.K.
Lüderitzbucht, S.W.A.	Budde-Lund, Panning, U.C.T., B.K.
Orange River mouth	U.C.T., B.K.
Hondeklip Bay	Barnard, U.C.T.
Groenriviermond	B.K., U.C.T.
Lambert's Bay	B.K., U.C.T.
Paternoster	B.K.
Saldanha Bay, Langebaan	Barnard, B.K., U.C.T.
Ysterfontein	B.K.
Melkboschstrand	Barnard, B.K.
Blouberg, Milnerton	Barnard, B.K.
Hout Bay	B.K., U.C.T.
Noordhoek	B.K., U.C.T.
Olifantsbosch	B.K.
Witsands Bay	B.K.

TABLE 2

Collecting localities for *Tylos capensis*

Locality	Collector
Simonstown	Budde-Lund
Muizenberg	Barnard, B.K.
Strandfontein	B.K.
Macassar Beach	B.K.
Somerset Strand	Barnard, Stebbing
Gordon's Bay	Stebbing
Pringle Bay	B.K.
Kleinmond	Barnard
Wilderness	Barnard
Breede River estuary	B.K.
Keurbooms River mouth	Barnard
Knysna	B.K., U.C.T.
Plettenberg Bay	Barnard, B.K.
Whitney	S.A. Museum
Port Elizabeth	B.K.
East London	S.A. Museum
Natal	Natal Museum

TABLE 3
Weight of food eaten by adult *Tylos* at single feeding session

Length (mm)	Prefeeding weight (g)	Postfeeding weight (g)	Weight eaten (g)	Volume (cc)	Wt eaten Body wt $\times 100$
47	7,622	8,785	1,163	1,2	15,26
44	5,523	6,667	1,144	1,3	20,71
43	5,175	6,357	1,182	1,2	22,83
42	5,291	6,163	0,872	0,9	16,47
41	4,154	5,181	1,027	1,0	24,73
41	5,276	6,297	1,021	1,1	19,35
39	4,112	5,004	0,892	0,8	21,70
38	4,097	5,144	1,047	1,0	25,55
38	4,037	4,918	0,881	0,9	21,82
37	3,912	4,614	0,702	0,6	17,95

TABLE 4
Food list of *Tylos granulatus*
(Only substances observed to be eaten included)

	Vegetable matter	Animal matter
<i>Phaeophyta</i>		Haarder
<i>Ecklonia maxima</i>	Cabbage	Joseph shark
<i>Laminaria pallida</i>	Onion	Nudibranchs
<i>Macrocystis pyrifera</i>	Orange	Gastropod egg cases
	Watermelon	Horny branchiopod shells
<i>Chlorophyta</i>	Bread	Jellyfish
<i>Bryopsis</i> sp.		Portuguese Man-of-War
<i>Codium fragilae capense</i>		Red bait tests
<i>Enteromorpha</i> sp.		Cormorant
<i>Ulva</i> sp.		Tern
<i>Rhodophyta</i>		
<i>Aristothamnion purpuriferum</i>		
<i>Botryoglossum platycarpus</i>		
<i>Carrodaria virgata</i>		
<i>Carpoblepharis flaccida</i>		
<i>Ceramium planum</i>		
<i>Champia lumbricalis</i>		
<i>Gigartina stiriata</i>		
<i>Gymnogongrus dilatatus</i>		
<i>Gymnogongrus vermicularis</i>		
<i>Phyllemania hieroglyphica</i>		
<i>Plocamium cornutum</i>		
<i>Porphyra capensis</i>		
<i>Pterosiphonia cloiophylla</i>		
<i>Suhria vittata</i>		
	Food list of <i>Tylos capensis</i>	
<i>Phaeophyta</i>	Sour fig leaves	Cormorant
<i>Ecklonia maxima</i>	<i>Ruppia maritima</i>	Haarder
<i>Laminaria</i> sp.	Watermelon	Hydroid perisarc
<i>Sargassum heterophyllum</i>		
<i>Chlorophyta</i>		
<i>Caulerpa</i> sp.		
<i>Codium fragilae capense</i>		
<i>Ulva</i> sp.		
<i>Rhodophyta</i>		
<i>Champia compressa</i>		
<i>Pterosiphonia cloiophylla</i>		
<i>Suhria vittata</i>		

TABLE 5
Food preferences of *Tylos granulatus*

31/7/68 Box Macrocystis	1	2	3	4	5	6	Total	Control	% Water loss
	—	—	1,481 0,000	—	—	—	1,481	—	—
Laminaria	1,670 0,000	—	1,481 —	—	—	1,515 1,024	2,161	1,471 1,433	2,6
Gigartina	1,670 —	—	—	—	—	0,491 1,869 1,571	0,298	0,038 1,653 1,494	9,6
Cabbage	1,096 1,075	—	—	1,129 1,039	—	0,298 —	0,111	0,159 0,908 0,823	9,1
Ulva	0,021 —	1,985 2,100 1,974	2,100 1,934	0,090 2,159 1,930	—	1,778 1,682	0,502	0,085 1,447 1,233	
Fish	2,071 0,000	0,011 2,100 0,880	0,166 1,956 0,000	0,229 2,520 0,000	2,221 0,000	0,096 2,814 0,747	12,055	0,214 3,745 3,677	1,8
	2,071	1,220	1,956	2,520	2,221	2,067		0,068	

TABLE 6
Food preferences of *Tylos granulatus*

	1	2	3	4	5	6	Total	Control	% Water loss
1/8/68									
Box	—	—	—	—	—	—	—	—	—
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	0,895	1,198	—	—	0,640	—	—	1,841	1,4
Cabbage	0,797	1,028	—	—	0,587	—	0,321	1,815	—
	0,098	0,170	—	—	0,053	—	—	0,026	—
Ulva	1,729	1,668	—	—	1,169	1,403	—	1,011	3,6
	1,619	1,460	—	—	1,005	1,265	0,510	0,964	—
	0,110	0,208	—	—	0,164	0,138	—	0,037	—
Fish	1,933	2,100	2,085	2,520	1,849	1,748	—	1,708	4,0
	0,793	0,897	0,436	1,414	1,520	1,237	5,938	1,639	—
	1,140	1,203	1,649	1,106	0,329	0,511	—	0,069	—

TABLE 7
Food preferences of *Tylos granulosus*

	1	2	3	4	5	6	Total	Control	% Water loss
2/8/68 Box	—	—	—	—	—	—	—	—	—
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	0,019	1,231 1,178	4,3
Cabbage	0,840 0,821	—	—	—	—	—	—	—	—
	—	—	—	—	—	—	0,123	0,053 1,230 1,061	—
Ulva	—	—	—	—	—	0,834 0,711	—	—	—
	—	—	—	—	—	—	0,123	0,169	—
Fish	2,633 2,485	1,689 1,426	1,878 1,607	—	2,020 1,796	—	0,906	1,793 1,696	5,4
	0,148	0,263	0,271	—	0,224	—	—	0,097	—

TABLE 8
Food preferences of *Tylos granulatus*

	1	2	3	4	5	5	Total	Control	% Water loss
5/8/68									
Box	—	—	—	—	—	—	—	—	—
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	—	—	—
Cabbage	—	—	0,737	—	—	—	0,061	1,097	7,4
			0,676	—	—	—		1,016	
Ulva	—	—	0,061	—	—	—	0,185	0,081	
			1,883	—	—	—		1,682	
			1,698	—	—	—		1,492	11,3
Fish	1,612	—	0,185	—	—	—	0,114	0,190	
	1,593	—	2,230	—	—	—		2,262	3,9
			2,215	—	—	—		2,173	
	0,099		0,015	—	—	—		0,089	

TABLE 9
Food preferences of *Tylos granulatus*

	1	2	3	4	5	6	Total	Control	% Water loss
8/8/68									
Box	—	—	—	—	—	—	—	—	—
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	1,965	1,771	—	—	1,888	—	1,377	2,130	1,5
Cabbage	1,670	1,455	—	—	1,122	—	—	1,833	—
	0,295	0,316	—	—	0,766	—	—	0,297	—
Ulva	2,067	2,339	1,534	1,900	2,252	1,625	4,344	2,254	13,9
	1,657	1,410	1,334	0,788	0,847	1,337	—	2,220	—
	0,410	0,929	0,200	1,112	1,405	0,288	0,019	0,034	6,7
Fish	—	—	1,810	—	—	—	—	2,085	—
	—	—	1,791	—	—	—	—	1,944	—
	—	—	0,019	—	—	—	—	0,141	—

TABLE 10

Dry/fresh brown alga (*Ecklonia*) preference test

Date		Box 1	Box 2	Control	Total eaten (g)
16/9/68	Dry	1,413	1,455	1,754	0,337
		1,263	1,268	—	
	Fresh	0,150	0,187	—	
		2,445	2,647	2,611	
18/9/68	Dry	1,475	1,377	1,580	0,077
		1,398	—	—	
	Fresh	0,077	—	—	
		2,424	1,956	2,192	
20/9/68	Dry	1,586	1,611	1,863	0,363
		1,381	1,453	—	
	Fresh	0,205	0,158	—	
		1,932	2,289	1,849	
22/9/68	Dry	1,711	1,623	1,695	0,265
		—	1,358	—	
	Fresh	—	0,265	—	
		1,981	2,035	2,107	
25/9/68	Dry	1,349	1,392	1,512	0,130
		1,219	—	—	
	Fresh	0,130	—	—	
		2,193	2,401	2,385	
28/9/68	Dry	1,604	1,449	1,449	0,064
		—	1,385	—	
	Fresh	—	0,064	—	
		2,035	1,991	1,941	

TABLE 11
Food preferences of juvenile *Tylos*

15/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Fish	0,539	0,616	0,602		
	0,495	0,488	0,599		
	0,044	0,128	0,003	0,172	4,2
Ulva	0,441	0,429	0,460		
	0,368	—	0,419		
	0,073	—	0,041	0,073	9,1
Plocamium	0,504	0,481	0,490		
	0,464	0,449	0,464		
	0,040	0,032	0,026	0,072	5,4
Macrocystis	0,771	0,754	0,798		
	—	—	—	—	—
Cabbage	0,681	0,703	0,665		
	—	0,642	0,611		
		0,061	0,053	0,061	8,0

TABLE 12
Food preferences of juvenile *Tylos*

17/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,388	0,413	0,409		
	0,327	0,363	0,367		
	0,061	0,050	0,042	0,111	10,3
Plocamium	0,453	0,420	0,484		
	—	0,381	0,463		
		0,039	0,021	0,039	4,4
Macrocystis	0,683	0,703	0,698		
	—	—	—	—	—
Cabbage	0,535	0,613	0,550		
	—	—	—	—	—
Fish	0,477	0,522	0,492		
	0,369	0,496	0,474		
	0,108	0,026	0,018	0,134	3,8

TABLE 13

Food preferences of Juvenile *Tylos*

19/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,325	0,369	0,410	0,060	8,0
		0,309	0,388		
		0,060	0,032		
Plocamium	0,503 0,420	0,486	0,471	0,124	4,8
		0,445	0,449		
		0,083	0,022		
Macrocystis	0,705	0,720	0,684		
Cabbage	0,489 0,471	0,532	0,516	0,018	7,5
		—	0,477		
		0,018	0,039		
Fish	0,613 0,526	0,586	0,590	0,189	3,4
		0,484	0,570		
		0,087	0,020		

TABLE 14

Food preferences of juvenile *Tylos*

22/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,440 0,397	0,419	0,398	0,061	9,6
		0,401	0,360		
		0,043	0,038		
Plocamium	0,621 —	0,570	0,597	0,041	3,9
		0,529	0,574		
		0,041	0,023		
Macrocystis	0,580	0,694	0,689		
Cabbage	0,388 —	0,412	0,370	0,023	8,3
		0,389	0,340		
		0,023	0,030		
Fish	0,664 0,570	0,580	0,683	0,155	4,5
		0,529	0,652		
		0,094	0,031		

TABLE 15

Data for 36 consecutive days observation of *Tylos granulatus*

Date	Time emerged	Time returned	Hours out	Hours between returns
1/2/68	2050	2230	2,50	
2	2100	2300	2,00	24,67
3	2115	2330	2,50	24,50
4	2210	0015	2,25	24,83
5	2230	0030	2,00	24,16
6	2315	0130	2,25	24,83
8	0005	0210	2,00	24,67
9	0040	0230	2,00	24,33
10	0125	0305	1,50	24,58
11	0200	0330	1,50	24,41
12	0245	0420	1,50	24,83
13	0300	0330	0,50	23,16
	2045	2220	1,50	18,50
14	2045	2215	1,50	23,91
15	2045	2230	2,00	24,25
16	2045	2240	2,00	24,16
17	2045	2240	2,00	24,00
18	2045	2250	2,00	24,16
19	2030	2310	2,50	24,33
20	2150	2350	2,00	24,67
21	2200	0015	2,25	24,41
22	2245	0110	2,50	24,91
23	2340	0210	2,25	25,00
25	0020	0040	0,34	22,50
	2030	2230	2,00	21,83
26	2040	2310	2,50	24,67
27	2100	2240	1,75	23,50
28	2120	2315	2,00	24,58
29	2120	2345	2,25	24,50
1/3/68	2130	0020	2,70	24,58
2	2230	0100	2,50	24,67
3	2300	0130	2,50	24,50
5	0010	0210	2,00	24,67
6	0015	0215	2,00	24,08
7	0030	0220	2,00	24,08
8	0045	0250	2,00	24,50

TABLE 16

Data for observations on darkroom animals of *T. granulatus*

Date	Time emerged	Time returned	Individuals
24/2/68	2120-2145	0030	8 animals
25	2115-2215	2320	3 animals
26	—	—	
27	—	—	
28	0030	?	3 animals
29	0005	0150-2000	1, 2, 3, 6, 7, 11, 15, 16, 18, 21, 20
1/3/68	2250-2330	0040-0115	2, 3, 6, 8, 9, 7, 10, 11, 13, 15, 18, 19
2	—	—	
3	0045-1000	0156-0210	4, 6, 8, 10, 11, 13, 15, 18, 20
4	2040-2200	2230-2330	2, 4, 5, 6, 7, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20
5	—	—	
6	0100	?	
7	0250	0315	2
8	0105	0125-0130	2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 20, 21, 22

TABLE 17

Data for observations on *Tylos capensis*

Date	Time emerged	Time returned	Hours out	Low tide
15/1/70	0210	0335	1,40	0247
16/1/70	0315	0430	1,25	0416
19/1/70	2040	2255	2,25	2011
25/1/70	2245	0115	2,50	2304
28/1/70	2320	0150	2,50	0002
31/1/70	0140	0340	2,00	0222
4/2/70	2040	2325	2,75	2029
9/2/70	2305	0120	2,25	2343
11/2/70	2340	0210	2,50	0018
19/2/70	2025	2255	2,50	2055
27/2/70	2340	0215	2,25	0004
5/3/70	2005	2240	2,60	2012
6/3/70	2025	2310	2,75	2051
9/3/70	2220	0035	2,25	2238

TABLE 18

Numbers of oligochaete *Enchytraeus tylidus* present on adult and juvenile *Tylos granulatus*

Locality		Number of oligochaetes per individual <i>Tylos</i>						
		0	1	2	3	4	5	6
Blouberg	No. adults	—	2	5	—	1	1	1
	No. juveniles	9	1	—	—	—	—	—
Lambert's Bay	No. adults	—	2	2	3	2	1	—
	No. juveniles	7	2	—	1	—	—	—



INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.

Style manual for biological journals. Washington: American Institute of Biological Sciences.

MANUSCRIPT

To be typewritten, double spaced, with good margins arranged in the following order: (1) Heading, consisting of informative but brief title, name(s) of author(s), address(es) of author(s), number of illustrations (figures, enumerated maps and tables) in the article. (2) Contents. (3) The main text, divided into principal divisions with major headings; sub-headings to be used sparingly and enumeration of headings to be avoided. (4) Summary. (5) Acknowledgements. (6) References, as below.

Figure captions and tables to be on separate sheets.

ILLUSTRATIONS

To be reducible to 12 cm × 18 cm (19 cm including caption). A metric scale to appear with all photographs.

All illustrations to be termed figures (plates are not printed; half-tones will appear in their proper place in the text), with arabic numbering; items of composite figures to be designated by capital letters (A, B, C etc.).

REFERENCES

Harvard system (name and year) to be used: author's name and year of publication given in text; full references at the end of the article, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year.

For books give title in italics, edition, volume number, place of publication, publisher.

For journal articles give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination.

Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100-140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

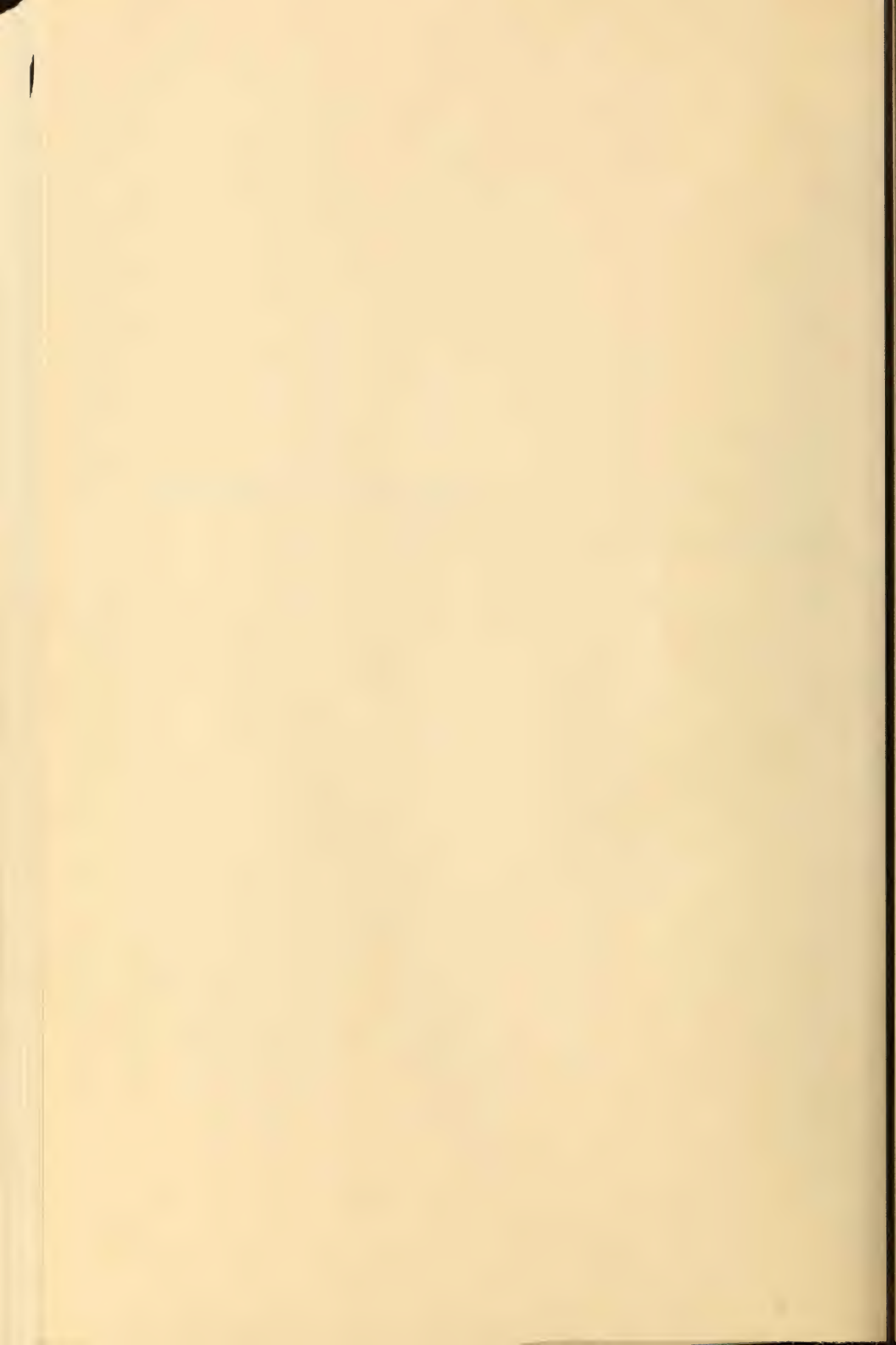
Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.



Brian Kensley

ASPECTS OF THE BIOLOGY AND ECOLOGY OF
THE GENUS *TYLOS* LATREILLE







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